HEAD MUSCULATURE OF SPHINX MOTHS[1]

(LEPIDOPTERA:SPHINGIDAE)

By

Richard C. Fleming[2]

ABSTRACT

An understanding of the myology of the adult head, as it occurs in the family Sphingidae is presented. All head muscles, exclusive of the intrinsic muscles of the proboscis, antenna, and labial palps, are described and compared for 15 species, representing 12 genera, and five subfamilies.

Muscles are classified into groups and homologies are shown wherever possible. Emphasis is placed on the role of head muscles used in the feeding process. It is established that some of the muscles associated with feeding are reduced in number and/or size in moths studied of the subfamily Smerinthinae and of the genus Ceratomia of the subfamily Sphinginae. These moths are no longer capable of feeding activity.

It is further established that, on the basis of the evolution of head musculature, the subfamily Smerinthinae is farthest removed from the hypothetical sphingid ancestral type.

INTRODUCTION

It is surprising that, despite the great popularity of the Lepidoptera with amateur and professional entomologists so little work has been done on the morphology of the group. This is especially true of comparative internal structure. Scattered information concerning internal structure occurs in the literature and general text books, but comprehensive work has been sadly neglected.

Probably the most significant study, which treats the comparative morphology of feeding mechanisms in several families of moths and butterflies, is that of Schmitt (1938). More recently Ehrlich and Ehrlich (1962, 1963) have published papers that deal respectively with the head musculature and thoracic musculature of butterflies. The orientation of these papers is, however, taxonomic rather than morphological, their intent being to arrest the erroneous notion that non-skeletal features can be ignored with reference to the classification of butterflies.

This investigation demonstrates that many species of sphinx moths do not feed as adults. General texts usually indicate that adult sphinx moths are nectar feeding insects. Ross (1965) states, "The moths are extremely rapid fliers and feed on nectar." Borror and DeLong (1964) say, "Most of them feed much like hummingbirds, hovering in front of a flower and extending their proboscis into it..." Comstock (1924) states, "As a rule they ...have the habit of remaining poised over a flower while extracting the nectar..." Matheson (1951) comments, "They are common visitors at flowers, sucking up the nectar with their long tongues."

While such statements are not completely untrue, generalization in this respect should be avoided for it appears that many adult sphinx moths are not morphologically equipped for feeding.

Field observations, strongly reinforced by the internal and external morphological evidence to be presented here, substantiate the hypothesis that probably neither the Smerinthinae examined nor Sphinginae of the genus Ceratomia feed as adult insects.

This work presents the myology of the head as it occurs in the family Sphingidae. The mechanisms involved in the feeding process, classification of the head muscles into logically arranged groups, muscle homologies, and the similarities and differences of muscles between 15 species, 12 genera and five subfamilies are discussed. It represents the first comparative study of several species of moths in one family.

THE CRANIUM

Few definitive statements concerning the musculature of the sphinx moth head can be made without some appreciation of the integumental anatomy. The sphinx moth cranium is similar in most respects to that of other lepidopterans and a fair understanding of its morphology may now be attained. Differences between the crania of the five subfamilies of sphinx moths are minor.

The literature contains several partial discussions and illustrations for various groups of Lepidoptera, the most comprehensive being the work of Schmitt (1938). Other noteworthy works include those of DuPorte (1946), Madden (1944) on Manduca (=Protoparce) sexta, Short (1951) on Dilina tiliae, DuPorte (1956) on Danaus archippus and Manduca quinquemaculata, Ehrlich (1958) on Danaus archippus, Ehrlich (1960) on Epargyreus clarus, and Michener (1952) on Saturniidae.

Other works that deserve attention, but do not limit themselves to the crania of Lepidoptera are Snodgrass (1935, 1947, 1960), Ferris (1943), Cook (1944), and Matsuda (1965).

The cranium of the lepidopterous head is a rather simple structure and only a few sutures are present.

Figures 1-3 represent a generalized view of the cranium and illustrate the intrinsic pump muscles, pump dilator muscles, the salivary duct, the muscles of the salivarium, and the position of the brain and subesophageal ganglion. Figure 4, another generalized drawing, represents a ventral view of the cranium and shows the ventral sclerites and the position of the muscles of the labial palps.

At least two drawings, a side view of the cranium with the eye removed, and a frontal view with a major portion of the facial sclerites removed, are

presented for each species. The former illustrates the proboscis extensor muscles and the antennal muscles, while the latter shows the positions of the sucking pump dilator muscles and such cranial features as sutures, inflections, mandibles, position of the anterior tentorial pits, and the labrum. Features not pertinent are omitted from the drawings which are somewhat diagramatic and designed to aid the reader in a quick interpretation of the material discussed in the text. Drawings of the same species are in approximate scale to one another, but drawings of different species are not.

The clypeus (Fig. 1) forms an area on the lower part of the face and is not clearly distinct from the frons. This fact has given rise to considerable debate as to which part represents the clypeus and which part the frons. While it is not the purpose of this paper to engage in a lengthy discussion concerning this point, it is of practical significance to indicate the present consensus. For many years the view held by Snodgrass (1935) and others that the facial sclerites may be interpreted properly by examination of cibarial and pharyngeal muscles, using them as landmarks, was, and still is, popular. Thus, in the lepidopterous cranium, the area anterior to the suture that extends between the antennal sockets would be the clypeus, as the cibarial muscles originate from it. The muscles posterior to the frontal ganglion are clearly the pharyngeal muscles, and their origin falls on a sclerite posterior to the suture between the antennae, and this would be the frons. Short (1951) follows this interpretation. In terms of generality the view is a solid one but the possibility of exceptions must be recognized.

Certain doubt, however, has been cast upon the advisability of using muscles as landmarks. Cook (1944) indicates that the cranial muscle origins are relatively independent of ectodermal structures and origin, alone, cannot be used for interpretation. Origins of muscles, positions of sutures, and fixed points must be taken into consideration in relation to morphological possibilities. DuPorte (1956) maintains that,

"Muscles are purely functional units and their mechanical
    efficiency depends in large part on their point of origin in
    the skeleton. With changes in the form or in the direction
    of growth of the organs they must often shift their origins
    even if this involves crossing a secondary inflection."

Another interpretation, adopted by Michener (1952) and based on DuPorte (1946), holds that the trilobed structure, usually considered the labrum, is, in reality, the reduced clypeus of the lepidopterous head, and the area posterior to it the frons, with the cibarial muscles shifted to that structure. This interpretation does not seem very likely.

Ferris (1943) questions the validity of the word "frons" in any insect, indicating that it means only a facial portion of the antennal segment and does not designate any separate morphological element.

The interpretation of DuPorte (1956) and the terminology used by him will be followed largely in this paper. It should be pointed out that in his 1956 paper he rejects the interpretation he set forth in 1946. He states (1956) that in Manduca two sets of cibarial muscles (muscles 1 and 2 in the present work) originate from what is clearly the clypeal region, one pair (muscle 3) originates from what is probably the frons but could be interpreted as the clypeus, and another pair (muscles 4 and 5) originate from an area that cannot be interpreted as the clypeus.

I have considered that area from where muscles 1 and 2 originate

the clypeal area, that area posterad of it and extending to the suture connecting the antennal sockets, the frontoclypeal area (Fig. 1), and that area just posterad of the suture, the frontal area (Fig. 1).

The transfrontal suture (Fig. 1) extends between the antennal sockets. The laterofacial suture (Fig. 1), a continuation of the transfrontal suture, extends ventrad from the antennal sockets to the clypeolabral suture which is a mesal extension of the laterofacial suture on either side. A transclypeal band (Fig. 1) meets the extension of the laterofacial suture at a point even with the base of the anterior tentorial pits which lie in the laterofacial suture just above the outer edges of the labrum. The laterofacial suture is inflected within the cranium as the laterofacial inflection (Fig. 1), to which certain cranial muscles attach. In Celerio lineata the inflection is considerably larger than in other species examined.

In all species studied the bulging compound eyes extend below the base of the cranium. The crania in Sphinginae, Choerocampinae, and Philampelinae are rather elongate and large in relation to the rest of the body. In Macroglossinae the head is somewhat smaller in relation to the rest of the body, and in Smerinthinae it is decidedly smaller and less elongate than in any other subfamily.

The three lobed labrum is comparatively small. (Fig. 1). The longer outer lobes represent the pilifers (Fig. 1, 4) while the inner lobe represents, in part, the epipharynx (Madden, 1944, and others). Little variation exists in the labrum among sphingid species but it is noteworthy that in Celerio lineata, on the lateral edges of the pilifers and firmly united with them, are small, elongate structures which were not present in any other sphinx moths studied. They are lightly sclerotized at their proximal end where they unite with the pilifers.

The mandibles (Fig. 1, 4) are fixed. They are rather prominent in some sphinx moths and in some species free from the cranium, except at the base. They are considerably reduced in Smerinthinae. It is of historical interest that at one time the pilifers were considered the mandibular bursas. Rothschild and Jordan (1907) indicated the incorrectness of calling these structures mandibles. They termed the true mandibular remnants "Wangenfortsatz." (Genal "cheek" processes.)

In sphinx moths the proboscis varies from very highly developed to degenerate. It may range in length, depending on species, from two to 90 millimeters (Table III). Moths of the genus Manduca and the closely allied genus Herse possess the most strongly developed proboscises of North American sphingids investigated. In Smerinthinae and a few Sphinginae (Ceratomia and Lapara) it is reduced and probably non-functional. Forbes (1948) noted the reduction of the structure in these groups and Rothschild and Jordan (1907) recognized the reduction of the proboscis in some Smerinthinae and the genus Ceratomia. Tillyard (1923) showed that the proboscis in Lepidoptera is derived from the galeae. Each half of the proboscis, where it is functional, forms the sides of a tube, the lumen of which is continuous with the body cavity through the stipes. Burgess (1880a) indicates each proboscis unit is rendered flexible by a series of fine rings separated by a membrane. Schmitt (1938) notes that in butterflies and higher moths the rings are made up of many small, flat circles of hard cuticula. The food channel is lined with similar rings but they have only about one third the width of the outer rings. Burgess (1880a) suggested that the coiling of the proboscis is effected by the action of muscles passing

obliquely between the rings. Berlese (1910) confirmed this finding. It was
not until 1938 that the functional mechanism of the uncoiling action of the
proboscis was described by Schmitt, although the suggestion that blood
pressure might be the uncoiling agency was first suggested by Snodgrass
(1935). Schmitt (1938) describes the activity as dependent on the action of
the proboscis extensor muscles (9 and 10 in the present paper) which insert
on the flat, mesal sclerite of the stipes. A valve arrangement lies between
this flat sclerite and the outer, tubular part of the stipes. As the muscles
pull the stipes upward the valve closes, and the tubular part becomes a
closed cylinder. In this manner pressure is exerted upon the blood in the
stipes cylinder, and as the stipes is closed at its proximal end, the blood
is forced outward through the stipes toward the proboscis. The posterior
proboscis extensor muscle (11) attaches to the stipes near the base of the
proboscis. Contraction of this muscle influences pressure on the blood
within the stipes cylinder and also raises the base of the proboscis unit,
bringing it in close contact with the stipes and effecting a tight seal with
the functional mouth. Blood is forced out into the lumen of the proboscis,
causing it to unroll. Schmitt points out that in many Lepidoptera the
stipital cylinder may be modified, but the principle is invariably the same.
He further states that the musculature concerned with extension of the
proboscis consists of three basic pairs, but that in a large number of
species one or two pairs may be absent. Functional maxillae always have
at least two pairs.

A series of careful observations and experiments by Eastham and
Eassa (1955) cast doubt on the "inflation" theory of Schmitt. They show
that in the butterfly Pieris brassicae proboscis extension is the result of
the contraction of oblique muscles within the proboscis coupled with the
formation of a closed haemocoele in that structure. Further they contend
that a fold at the base of both galeae prevents the passage of fluid from the
galea to the head and that the stipital aperture is constructed so that a
closed galeal haemocoel can result. In light of their findings it is apparent
that more investigation of the extension mechanism of the proboscis is
necessary.

In sphinx moths, as in most other Lepidoptera, the stipes (Fig. 4)
shows clear division into two parts; a folded, tubular lateral part, and a
flattened mesal part. The stipes is reduced in Smerinthinae.

The cardo (Fig. 4) is a small, immovable sclerite bordered laterad
by the gena, anteriad by the stipes, and posteromesad by the labial
sclerite (Fig. 4).

Arising on the stipes, near the proboscis base, are the tiny, one
segmented maxillary palps (Fig. 4). Forbes (1948) states that the maxil-
lary palps are absent in sphinx moths.

The labium is composed of a sclerite that extends from the well
developed hypostomal bridge (Fig. 4) to the base of the proboscis. Much
of it, especially the lateral parts, is only lightly sclerotized, but the area
of heaviest sclerotization varies with different species. It is bordered by
the gena at the level of the three segmented labial palps (Fig. 4), and by
cardo and the stipes anterior to the labial palps.

The most highly developed parts of the tentorium are the anterior
arms. (Fig. 3). There are no dorsal arms. Schmitt (1938) indicates
that dorsal arms do not occur in any adult Lepidoptera. In most cases,
among Sphingidae, the anterior arms are rather straight. In the

Philampelinae, feeding members of the Sphinginae, Macroglossinae, and Choerocampinae they possess ventral and dorsal raised portions that afford broad muscle attachment surfaces for the powerful proboscis extensor muscles and antennal muscles respectively. Many of these insects also possess a lateral ridge on the anterior arms that affords even more muscle attachment surface as well as extra structural strength to the arms. In the Smerinthinae only the dorsal raised portion of the arm is present. It is noteworthy that this group does not possess all three pairs of proboscis extensor muscles as found in species with fully functional mouth parts. Only the posterior proboscis extensor muscle remains, and that is considerably reduced. The ventral swellings of the anterior arms are very slight in the Sphinginae which do not have strongly developed proboscis extensor muscles (genus Ceratomia).

In the smerinthine species Cressonia juglandis the anterior arms have a distinctive horizontal "S" shape not present in other sphinx moths examined. (Fig. 23).

In all sphinx moths the anterior arms are united posterad by a rather narrow tentorial bridge. Where the tentorial bridge and the tentorial arms come together, one finds, in the postoccipital region of the cranium, the posterior tentorial pits.

The posterior tentorial arms are evidently incorporated into the flared area where the pits enter the postoccipital suture. In the Smerinthinae, when viewed from below, the hypostomal bridge, labial palps, labium, cardo, and stipes are shifted anterad so the tentorial bridge is clearly visible (Fig. 5). This condition is not present in any other sphinx moth subfamily.

In all sphinx moths good structural support is rendered to the ventral and posterior part of the cranium by the well developed hypostomal bridge. The small tentorial bridge probably offers little help in this respect.

It should be noted that in a comparatively thin structure like the cranium, a danger of buckling exists. This is especially true in certain insects, including sphinx moths, with powerful cranial muscles. Short (1951) indicates that the inward inflection of the transfrontal suture (his "epistomal ridge") safeguards against this buckling. Other ridges and inflections, including the postoccipital ridge (Fig. 2) and laterofacial inflection, as well as the tentorium and the curvature of the cranium itself, render sufficient resistance to buckling.

THE HEAD MUSCLES

The literature on the musculature of the head of sphinx moths is not extensive, and, until the present work, no attempt has been made to compare the morphology of several species of the family. Berlese (1910) described and illustrated to some extent the muscles of the head of Sphinx convolvuli. Snodgrass (1935) described and illustrated some of the sucking pump muscles of "a sphinx moth." Schmitt (1938) illustrated and discussed head muscles in several species, including Darapsa pholus, Haemorrhagia thysbe, and Smerininthus geminatus. Short (1951) illustrated some of the head muscles of Dilina tiliae. DuPorte (1956) pictured sucking pump muscles of Manduca quinquemaculata. Matsuda (1965) illustrates some of the head muscles of a sphinx moth.

The following muscle group discussion and description includes all muscles of the sphinx moth cranium exclusive of the intrinsic muscles of the proboscis and the antennae. Muscle numbers indicate suspected and obvious homologies between the species. Muscle differences are pointed out in Tables I and II, in the figures, and in the discussions of the sub-families. Figures 1-4 represent a generalized condition.

Dilator muscles of the sucking pump (Muscles 1, 2, 3, 4, 5)

This group of muscles is the principal set used in expanding the sucking pump. They are better developed in species with strongly developed feeding mouth parts than in those with degenerate mouth parts. Muscle 5 may be absent.

Muscles of the wall of the sucking pump (Muscles 6, 7)

Muscle 6 is really a complex of several muscle bands that obviously constrict the pump. The oral valve muscle, 7, apparently constricts the oral opening and probably keeps ingested juices from escaping when they are forced into the digestive tract. While 7 may be considered one of the intrinsic pump muscles, it is always distinct from the rest. It is similar in all Sphingidae.

Histological sections of the pumps of Paonias myops and Manduca sexta clearly showed the muscular nature of most of that organ. Schmitt (1938) established that the muscles in Danaus menippe are arranged in two double-layered groups, one group transverse and the other longitudinal. My own studies did not clearly demonstrate this arrangement to be the case in Sphingidae, but there is little doubt of the several layered nature of the pump walls. Since dilator muscles, themselves, contribute to some of the pump musculature I am in agreement with Schmitt that some of the intrinsic pump muscles could have been derived from them.

The sucking pump of most Lepidoptera is rather well developed, although it may be considerably reduced in non-feeding species. One of the first descriptions of the pump was offered by Kirbach (1883), using Nymphalis io. Burgess (1880b) and Kellogg (1893) considered the same subject in the monarch butterfly. But the morphology of the pump was not understood until later. Snodgrass (1935) stated that no definite statement can be made as to the morphology of the sucking pump of Lepidoptera without further study, but he indicates that the pump includes at least the buccopharyngeal region of stomodaeum. It should be noted that the dilators of that organ (muscles 1-5) are inserted on it, both anteriad and posterad of the frontal ganglion. This phenomenon is helpful in determining which part of the pump is cibarial and which pharyngeal. Schmitt (1938) offers good evidence that at least part of the pump is composed of the cibarium, that structure defined by Snodgrass (1935) as,

"The food pocket of the extraoral or preoral mouth cavity between the base of the hypopharynx and the under surface of the clypeus".

Schmitt points out that in orthopteroid insects a pair of muscles that compress the labrum originate on the anterior wall of the labrum and insert on the epipharyngeal wall. If the small lobe between the pilifers is the epipharynx, and it seems to be, this pair of muscles as it occurs in some Lepidoptera (apparently absent in sphinx moths) would indicate that the cibarium would then form the anterior section of the pump.

Schmitt offers other evidence that the cibarium is included in the pump, based on the structure of its floor. He notes that at the base of the salivary meatus, in numerous generalized insects, there is a cup-like depression into which products of the medial salivary duct are poured. This depression, the salivarium (Fig. 2) is supplied with three pairs of muscles, the dorsal pair arising on the suspensory sclerite of the hypopharynx. Of the three pairs this is the only pair that typically occurs in Lepidoptera. These muscles, 8, originate on the floor of the sucking pump in Lepidoptera, indicating that the anterior part of the floor is derived from the hypopharynx and therefore this portion of the sucking pump belongs to the cibarium. The floor of the pump is heavily sclerotized in the Sphingidae.

The insertions of muscles 4 and 5, posterior to the frontal ganglion, indicate that that part of the pump is the pharynx, as it is in certain other insects (including Hymenoptera).

Muscle of the salivarium (Muscle 8)

This muscle evidently exerts some control over the release of salivary secretions from the salivarium. It is very weakly developed in non-feeding sphinx moths.

Proboscis extensor muscles (Muscles 9, 10, 11)

Muscles 9 and 10 raise the stipes and the role they play in proboscis extension has been previously described. Muscle 11 is involved with the creation of blood pressure within the stipes and the raising of the proboscis base.

The maximum number of proboscis extensor muscles found in adult Lepidoptera is three pairs. In all sphinx moths with functional mouth parts this is the case, and muscle 9 is frequently the largest muscle in the head. It may obscure most of the antennal muscles from lateral view. In sphinx moths with degenerate, and apparently non-functional mouth parts, muscles 9 and 10 may be reduced in size or absent. Muscle 11 is always present but may be reduced in size.

Antennal muscles (Muscles 12, 13, 14, 15, 16)

In the Sphingidae four or five antennal muscles may be present. When only four are present, muscle 15 is absent. Elevation of the antennae is accomplished by the action of muscles 12 and 13, while depression is accomplished by muscles 14, 15, and 16. The positions and configuration of the antennal muscles represent a highly functional, well balanced system.

As in all groups of Lepidoptera, homologizing of antennal muscles in sphinx moths is not easy and I recognize the fact that I may be in error with some of the interpretations here presented, especially with reference to the Smerinthinae in comparison with other subfamilies.

Muscles 12, 13, and 16 would seem obviously homologous between all smerinthine sphinx moths, and in fact, between all sphingid species regardless of subfamily. Muscles 14 and 15, however, are less obviously homologized between smerinthines and other sphinx moths. Cook (1944) presents evidence that insertions of muscles are always consistant and never shift their morphological relations and are, as far as known, absolutely dependent upon structures which they move. Thus muscle homologies may be judged best on the basis of their insertions.

The antennal muscles considered to be homologous in the present work

were judged on the basis of their insertions and relative positions. Both criteria, although not infallible, should, in this case be valid, as the well balanced muscle system of the antenna could not have its muscle components shifted very much and still operate. The position of the antennae themselves do not shift in sphinx moth species.

Muscles of the labial palps (Muscles 17, 18)

Muscle 17 apparently moves the palp outward and depresses it, while muscle 18 elevates that structure.

Schmitt (1938) indicates that the presence or absence of labial palpal muscles is a variable situation among lepidopterous families, but that the number is never more than two. My observations agree with this. Schmitt further states that sphinx moths may have one or two palpal muscles and one is the usual case. The present study indicates that most sphinx moths have two muscles per palp, (Table II), although muscle 18 may be extremely reduced and easily overlooked.

While it is assumed that the origin of muscle 17 is on a part of the labial sclerite, it is possible that this area represents an anterior extension of the hypostomal bridge. There is no clear way of demarking the posterior edge of the labium, and the origin of the palpal muscles cannot be used as a guide for determination of the sclerotized area. Schmitt (1938) showed that muscle 17 (his depressor muscle of the labial palp) may originate on the labial sclerite or the hypostomal bridge in Lepidoptera. Ehrlich and Davidson (1961) indicate that this muscle originates on the labial sclerite in Danaus archippus.

MUSCLE DESCRIPTION

1. Anterior cibarial dilator muscle (Figs. 1, 2) This unpaired but short and broad muscle arises on the lower portion of the clypeal area of the cranium and inserts on the cibarial portion of the sucking pump, anterad of other cibarial dilator muscles.

2. Medial cibarial dilator muscle (Figs. 1, 2) This paired, well developed muscle is frequently divided into two parts. It arises laterad of the mid line on the clypeal region of the cranium, posterad of 1 and inserts on the cibarial part of the sucking pump, opposite of its point of origin.

3. Posterior cibarial dilator muscle (Figs. 1, 2) This paired, flattened, heavy, frequently divided muscle is variously developed depending on species but it is always the largest of the cibarial dilator muscles. It may originate on the laterofacial inflection, the antennal ridge, or a point on the cranium just posterad of the transfrontal ridge, or on a combination of these. It inserts on the dorsomesal region of the cibarial portion of the sucking pump.

4. Lateral pharyngeal dilator muscle (Figs. 1, 2) A paired, rather slender muscle that arises on the cranium posterad of the transfrontal suture, posterad and laterad of muscle 3 and inserts on the pharyngeal part of the sucking pump.

5. Medial pharyngeal dilator muscle (Figs. 1, 2) This small muscle may be paired, unpaired, or absent. It originates on the frontal part of the cranium posteromesad of 4 and inserts on the pharyngeal part of the

sucking pump, mesad of the insertion of 4.

6. Intrinsic pump muscles (Fig. 2) These heavy muscle bands are arranged in layers and, in conjunction with the dilator muscles, themselves, contribute to the walls of the sucking pump.

7. Oral valve muscle (Fig. 2) This well developed muscle extends across the anterior part of the pump.

8. Salivarium muscle (Fig. 2) This paired, usually small muscle extends from the hypopharynx to the salivarium.

9. Cranial proboscis extensor muscle (Fig. 3) This large, fan shaped muscle arises on the laterofacial part of the cranium along the laterofacial inflection and inserts on the flat, mesal sclerite of the stipes, laterad of other proboscis extensor muscles. It is absent in some species.

10. Anterior proboscis extensor muscle (Fig. 3) This frequently powerful muscle arises on the lateral and ventral surfaces of the anterior arm of the tentorium and inserts on the mesal sclerite of the stipes, just mesad of the insertion of 9. It may be absent in some species.

11. Posterior proboscis extensor muscle (Fig. 3) This well developed muscle arises on the mesal surface of the anterior arm of the tentorium and inserts at a distal point on the stipes, mesad of 10.

12. Anterior antennal levator muscle (Fig. 3) This large fan-shaped muscle arises on the dorsal or dorsolateral surface of the anterior arm of the tentorium and inserts on the inner, lateral part of the scape.

13. Posterior antennal levator muscle (Fig. 3) This muscle, of similar shape, but always smaller than the other antennal muscles, arises on the dorsal surface of the tentorium, posterad of other antennal muscles, and inserts on the inner, posterior part of the scape.

14. Anterior antennal depressor muscle (Fig. 3) This strongly developed, fan-shaped muscle originates on the dorsolateral surface of the anterior arm of the tentorium and inserts on the inner, anterolateral part of the scape.

15. Posterior antennal depressor muscle (Fig. 3) This moderately developed, fan-shaped muscle arises on the dorsal surface of the tentorium and inserts on the inner, anterior part of the scape. It is absent in some species.

16. Mesal antennal depressor muscle (Fig. 3) This moderate to well developed, fan-shaped muscle arises on the dorsomesal surface of the anterior arm of the tentorium, mesad of other antennal muscles, and inserts on the inner, mesal part of the scape.

17. Anterior palpal muscle (Fig. 4) This rather small muscle originates on the labial sclerite and inserts along the proximal, inner surface of the first segment of the labial palp.

18. Posterior palpal muscle (Fig. 4) This muscle, which is usually smaller than 17, arises on the hypostomal bridge and inserts on the proximal, inner surface of the first segment of the labial palp. It is absent in some species.

Head Muscles in Sphinginae

Species selected for morphological examination included Manduca sexta (Johansson), Ceratomia undulosa (Walker), Ceratomia catalpae

(Boisduval), and Sphinx eremitus (Hübner).   Field observations show that M. sexta and S. eremitus, as well as other moths in those genera, are active feeders as adults.   On the other hand no member of the genus Ceratomia has ever been seen taking food.

While obvious homologies exist between the head muscles of the Sphinginae, it is noteworthy that one genus, Ceratomia, shows consider-able divergence from the basic pattern of the subfamily.   The divergence manifests itself primarily as a strong reduction in the size of some of the muscles.   The reduction in size of the muscles corresponds with the apparent non-feeding habits.

Dilator muscles of the sucking pump

In general the dilator muscles are well developed in all feeding species examined.   A figure in a paper by DuPorte (1956) of M. quinque-maculata shows considerable development of these muscles in that species. I suspect that all feeding members of this subfamily have strong dilator muscles.

In the genus Ceratomia the muscles are only moderately developed and, unlike other moths considered in the present study, there is notable individual variation in both extent and number of subdivisions of some of these muscles.

1. (Figs. 6, 8, 10, 14) In M. sexta this muscle is much more highly developed than in the other members of the Sphinginae examined.

2. (Figs. 6, 8, 10, 14) Clearly divided into two parts (2a, 2b) only in S. eremitus.   A slight to moderate tendency toward subdivision is evident in other species.   Less highly developed in C. catalpae and C. undulosa than in M. sexta and S. eremitus.

3. (Figs. 6, 8, 10, 11, 12, 14) A muscle divided into several parts depending on the species.   In M. sexta it is not divided and is very strongly developed.   In C. undulosa it is only moderately developed and undivided. There is some individual variation in this muscle in this species, it being less heavily developed in some individuals than in others.   In C. catalpae the muscle may be divided into two parts (3a, 3b), but in many individuals it is not.   The variations illustrated represent the most noteworthy ones. The muscle showed other conditions not readily categorized.   In some in-dividuals it was moderately developed, while in others it was less robust with only a few strands.   The tendency to split into several parts was greater in some specimens than in others.   In no other sphinx moth was muscle 3 so variable as in C. catalpae.   In S. eremitus the muscle, well developed, was divided into three parts, (3a, 3b, 3c).

4. (Figs. 6, 8, 10, 14) A muscle showing little variation among the species of Sphinginae.

5. (Figs. 6, 10, 14) Absent in C. undulosa.   Unpaired in S. eremitus. Paired in C. catalpae and M. sexta.

Muscles of the wall of the sucking pump

6. (Fig. 2) These muscles are least highly developed in the two representatives of the genus Ceratomia of all sphinx moths studied; a condition indicative of their loss of feeding ability.   In M. sexta and S. eremitus the intrinsic pump muscles are well developed.   Histological study of the pump of M. sexta clearly indicated the functional possibilities of the structure as a pumping organ.

7. (Fig. 2) Similar in all Sphinginae.

Muscle of the salivarium

8. (Fig. 2) A muscle weakly developed in C. undulosa and C. catalpae and rather strongly developed in M. sexta and S. eremitus. In fact, for moths used in this study, it was most highly developed in M. sexta.

Proboscis extensor muscles

9. (Figs. 7, 9, 15) In M. sexta and S. eremitus an extremely large muscle obscuring most of the antennal muscles. Its size is considerably reduced in C. undulosa and it is altogether absent in C. catalpae.

10. (Figs. 7, 9, 13, 15) A rather powerful muscle in M. sexta and S. eremitus, and much less powerful in C. undulosa and C. catalpae.

11. (Figs. 7, 9, 13, 15) In M. sexta and S. eremitus this muscle is quite extensive, but most of it is hidden from lateral view by the anterior tentorial arms themselves and the other proboscis extensor muscles. In C. undulosa and C. catalpae the muscle is less highly developed.

It is noteworthy that the cranial proboscis extensor muscles show a significant reduction in size in members of the genus Ceratomia. Proboscis extension would be difficult and not very efficient, if indeed, it were possible at all.

Antennal muscles

12. (Figs. 7, 9, 13, 15) Similar in all Sphinginae.

13. (Figs. 7, 9, 13, 15) Similar in all Sphinginae.

14. (Figs. 7, 9, 13, 15) In C. undulosa and M. sexta this muscle arises mesad of 12, while in C. catalpae and S. eremitus it arises laterad of 12. In C. catalpae it originates much farther anterad of the other antennal muscles. Such a wide separation of this muscle from the others has not been found in any sphingids.

15. (Figs. 7, 15) Absent in C. catalpae and C. undulosa.

16. (Figs. 7, 9, 13, 15) Similar in all Sphinginae.

Muscles of the labial palps

17. (Fig. 4) Except for minor size variation, similar in all Sphinginae.

18. (Fig. 4) Not present in C. catalpae.

Head Muscles in Smerinthinae

Species studied were Smerinthus geminatus (Say), Paonias excaecata (Smith & Abbot), Paonias myops (Smith & Abbot), Cressonia juglandis (Smith & Abbot), and Pachysphinx modesta (Harris). I have never observed feeding by any adults of this subfamily.

While the head musculature of the Smerinthinae shows variation within species of the group, homologies between the five species examined are readily apparent. Even when compared to other subfamilies, homologies are clear, but so are certain modifications which distinctly set this subfamily apart. The obvious non-feeding habits of these moths, and the corresponding reduction of feeding mouth parts are reflected to a significant extent by modifications of internal head components, including muscles.

An internal dissection of the digestive tract of P. myops disclosed the fact that the crop is absent, another indication that it is a non-feeder. The lack of a crop was in sharp contrast to the condition found in M. sexta (Sphinginae) whose digestive tract reveals a large crop existing as a diverticulum of the hind part of the stomodaeum.

Dilator muscles of the sucking pump

The muscles of the sucking pump show a strong tendency toward sub-division. They are always reduced in size as compared to other subfamilies (except the genus Ceratomia of the Sphinginae). But in some species the pump muscles are not so reduced as to rule out their ability to dilate the sucking pump. The reduction in size of the dilator muscles is greatest in C. juglandis. While the size reduction of the dilator muscles may be a significant factor in the lack of feeding ability, it is the reduction of mouth parts and reduction or absence of the proboscis extensor muscles that most clearly indicate that these species are not able to feed.

1. (Figs. 16, 18, 20, 22, 24) Similar in all Smerinthinae.

2. (Figs. 16, 18, 20, 22, 24) Divided into two parts in all species examined. Except in C. juglandis, where 2a and 2b are of equal size, 2a is smaller than 2b.

3. (Figs. 16, 18, 20, 22, 24) Divided in all species except P. excaecata where the division is not complete. In C. juglandis, P. modesta and S. geminatus the muscle is divided into three parts (3a, 3b, 3c). In C. juglandis and P. modesta the origin of the parts is similar, but S. geminatus shows some differences in this regard, as indicated by the figures and muscle summary. In P. myops the muscle is divided into two parts, (3a, 3b).

It is apparent that in all sphinx moths this muscle is the most power-ful and well developed of the sucking pump muscles. In the Smerinthinae it is not so heavily developed as in certain members of other subfamilies. In C. juglandis the poor development of this muscle is especially notable.

4. (Figs. 16, 18, 20, 22, 24) Similar in all Smerinthinae, but more highly developed in P. modesta than in the rest.

5. (Fig. 16) Absent in all Smerinthinae examined except S. geminatus, where it is small and paired.

Muscles of the wall of the sucking pump

6. (Fig. 2) Histological study of the pump of P. myops, which may be considered typical of the Smerinthinae with reference to the pump, demon-strated the muscular nature of that organ. It should be noted, however, that the intrinsic musculature of the pump is not nearly so well developed as in feeding species such as M. sexta (Sphinginae), wherein histological examination revealed heavy muscle development.

In Smerinthinae the pump takes up a great deal of room within the cranial capsule. The size of the pump of S. geminatus prompted Schmitt (1938) to comment,

"...this development of the sucking pump has reached such a point that little space is left for the brain and the sub-oesophageal ganglion."

While this might first appear to be the case I do not feel that the sucking pump in any of the Smerinthinae has reached the high point of development suggested by Schmitt. The apparent "crowding" of other

cranial components by the pump is evidently the result of the reduction of
the size of the cranium which is, in all Smerinthinae studied, considerably
smaller in proportion to the rest of the body than in other sphingid sub-
families. It is probably true that the size of the sucking pump in Smerin-
thinae is not reduced significantly from the size of the fully functional pumps
of their probable feeding ancestors. If one were to consider feeding in-
ability on the basis of pump morphology alone, one would easily conclude
that the pump of Smerinthinae could well be functional, but other morpho-
logical considerations point to the probability that the whole subfamily is a
non-feeding one.

Schmitt (1938) makes no direct reference to the fact that S. geminatus
is a non-feeding species, although he makes a general statement that fully
functional mouth parts must have at least two pairs of proboscis extensor
muscles.

In the course of the present investigation I found it possible to mis-
judge the size of the sucking pump. Besides individual variation, which
seems to be slight, it is possible to observe the pump in a dilated or con-
tracted state. If a specimen with the former preserved condition was under
observation, the pump, of course, would appear larger than if the alter-
native were the case.

7. (Fig. 2) Always distinct and similar except for minor size
variation in Smerinthinae.

Muscles of the salivarium

8. (Fig. 2) Small in all Smerinthinae with little specific variation.

Proboscis extensor muscles

9. and 10. Absent.

11. (Figs. 17, 19, 21, 23, 25) Rather small but present in all
Smerinthinae. This muscle was observed by Schmitt (1938) in S. geminatus.
He considered it to be the posterior proboscis extensor muscle, because of
its insertion. The present study supports Schmitt's conclusion.

The fact that none of the Smerinthinae examined have a full compli-
ment of proboscis extensor muscles, is evidence that they are non-feeders.
It is not conceivable that the proboscis extension mechanism could function
without either one more set of extensor muscles, or at least heavier develop-
ment of the single pair of muscles (11) than is present.

Antennal muscles

12. (Figs. 17, 19, 21, 23, 25) Similar in all Smerinthinae. In C.
juglandis the muscle diverged, somewhat, from the general smerinthine
pattern in that it was smaller and its origin was mostly on the dorsal,
rather than the dorsolateral surface of the anterior tentorial arm.

13. (Figs. 17, 19, 21, 23, 25) Only slight specific variation occurs.

14. (Figs. 17, 19, 21, 23, 25) Similar in all Smerinthinae.

15. (Fig. 23) Present only in C. juglandis.

16. (Figs. 17, 19, 21, 23, 25) Similar in all Smerinthinae.

Muscles of the labial palps

17. (Fig. 5) Similar in all Smerinthinae.

18. Absent in the Smerinthinae examined.

Head Muscles in Macroglossinae

Two species, Haemorrhagia thysbe (Fabricius) and Haemorrhagia diffinis (Boisduval) were selected for morphological studies. Field observation indicates that adults of both species are active feeders.

In the Macroglossinae the head muscles are so well developed that very little free space is present within the head capsule. The musculature agrees closely with that of feeding species in other subfamilies.

There is little difference between the two species with reference to head musculature. Schmitt (1938) examined the proboscis extensor muscles in H. thysbe.

Dilator muscles of the sucking pump
      1. (Figs. 26, 28) Virtually identical in both species.
      2. (Figs. 26, 28) Similarly divided into two parts (2a, 2b) in both species.
      3. (Figs. 26, 28) Highly developed in both species. In H. thysbe the muscle is usually divided into two distinct parts (3a, 3b), but the division may not always be complete. In H. diffinis the division of the muscle is not complete.
      4. (Figs. 26, 28) Moderately well developed and similar in both species.
      5. (Fig. 28) Apparently absent in H. thysbe, although one specimen showed an extra pharyngeal dilator muscle which appeared to be a subdivision of 4, as the division from 4 was not complete. In H. diffinis muscle 5 is distinct.

Muscles of the wall of the sucking pump
      6. and 7. (Fig. 2) Virtually identical in both species.

Muscle of the salivarium
      8. (Fig. 2) Similar in both species.

Proboscis extensor muscles
      9., 10., 11. (Figs. 27, 29) All very well developed and similar in both species.

Antennal muscles
      12. (Figs. 27, 29) Arising on the dorsal surface, in H. diffinis, or the dorsolateral surface, in H. thysbe, of the anterior tentorial arm. Similar in other respects in both species.
      13., 14., 15., 16. (Figs. 27, 29) All similar in both species.

Muscles of the labial palps
      17., 18. (Fig. 4) Similar in both species. 17 is the largest of the muscles.

Head Muscles in Philampelinae

Species examined were Pholus satellitia pandorus (Hübner), Ampeloeca myron (Cramer), and Amphion nessus (Cramer). Field study

shows that these species, as well as other members of the subfamily, feed as adults.

Head musculature in the Philampelinae is quite similar to that found in feeding members of other subfamilies. Muscles associated with the feeding structures are among the most highly developed of any sphinx moth group. Some of the head muscles of Darapsa pholus are figured by Schmitt (1938).

Dilator muscles of the sucking pump
        1. (Figs. 30, 32, 34) Similar in all Philampelinae examined.
        2. (Figs. 30, 32, 34) Not divided into two parts in A. myron and A. nessus, but divided into two parts (2a, 2b) in P. satellitia.
        3. (Figs. 30, 32, 34) An extremely well developed muscle in all three species and divided into two parts in each (3a, 3b) but the division in A. myron is quite different from the other two species. In A. myron muscle 3a is rather small while 3b is quite extensive and partly divided, that part originating on the frontal area of the cranium probably homologous with 3b in the other species, while that part originating on the antennal ridge is probably homologous with 3a in P. satellitia and A. nessus. Muscle 3b is more highly developed in P. satellitia than in A. nessus.
        4. (Figs. 30, 32, 34) Similar in the Philampelinae examined.
        5. (Figs. 30, 32, 34) Paired and similar in the three species.

Muscles of the wall of the sucking pump
        6., 7. (Fig. 2) Similar and well developed in Philampelinae.

Muscle of the salivarium
        8. (Fig. 2) Similar in all three species.

Proboscis extensor muscles
        9., 10., 11. (Figs. 31, 33, 35) All strongly developed and similar in Philampelinae.

Antennal muscles
        12., 13., 14., 15., 16. (Figs. 31, 33, 35) The five muscles, two levators and three depressors, form a similar and well balanced system in Philampelinae.

Muscles of the labial palps
        17., 18. (Fig. 4) These muscles are similar in Philampelinae examined. 18 is smaller than 17.

Head Muscles in Choerocampinae

        Celerio lineata (Fabricius) is the only member of the Choerocampinae that the author examined, so assumptions cannot be made about how typical the muscle arrangement of C. lineata is for the subfamily. It may be assumed, however, that the head musculature of this species is representative of the subfamily.

        The head musculature is extensive and all systems are well developed. This species feeds extensively as an adult, and its feeding capacity is

reflected in its anatomy.

Dilator muscles of the sucking pump

1. (Fig. 36) Rather small when compared to that of other feeding species.

2. (Fig. 36) Divided into two parts (2a, 2b). 2a is distinctly compressed laterally, not rounded as in most sphinx moths.

3. (Fig. 36) The largest and most powerful pump muscle in this species, as in the others. There is only a hint of subdivision into two parts.

4., 5. (Fig. 36) Muscle 5 is smaller than 4 and paired.

Muscles of the wall of the sucking pump

6., 7. (Fig. 2) Well developed in C. lineata.

Muscle of the salivarium

8. (Fig. 2) Rather small in this species.

Proboscis extensor muscles

9., 10., 11. (Fig. 37) All these muscles are strongly developed in this species. 9 arises mostly on the inner surface of the well developed laterofacial inflection.

Antennal muscles

12., 13., 14., 15., 16. (Fig. 37) Three depressors and two levators are present. This well balanced system is similar to that of other sphinx moths with five antennal muscles.

Muscles of the labial palps

17., 18. (Fig. 4) 17 is comparatively small in C. lineata. 18 is extremely small and easily overlooked.

COMPARATIVE SUMMARY OF HEAD MUSCLES
(Tables I, II)

1. Anterior cibarial dilator muscle: Because so little variation occurs in this muscle from species to species, no characteristics are assigned to it. Generally, it is more developed in feeding species than in non-feeding ones. It is never paired.

2. Medial cibarial dilator muscle: Variations:
A: Distinctly subdivided into two separated parts.
B: Subdivided into two parts but parts contiguous.
C: No subdivision.

3. Posterior cibarial dilator muscle: Variations:
A: Not subdivided.
    A.1: Origin on laterofacial inflection and antennal ridge.
    A.2: Origin on antennal ridge entirely.
    A.3: Origin on antennal ridge and frontal area of cranium.
    A.4: Origin on laterofacial inflection, antennal ridge and frontal area of cranium.

B: Subdivided into two distinct parts.
    B.1: Origin of first (anterior) division on laterofacial inflection
         only. Second division on antennal ridge only.
    B.2: Origin of first (anterior) division on laterofacial inflection.
         Second division on antennal ridge and frontal part of cranium.
    B.3: Origin of first (anterior) division on laterofacial inflection
         and antennal ridge. Second division on frontal region of
         cranium.
    B.4: Origin of first (anterior) division entirely on antennal ridge.
         Second division on frontal region of cranium.
C: Subdivided into three distinct parts.
    C.1: Origin of first (anterior) division entirely on laterofacial
         inflection. Second division on laterofacial inflection to
         antennal ridge. Third division entirely on antennal ridge.
    C.2: Origin of first (anterior) division on laterofacial inflection
         and antennal ridge. Second division on antennal ridge.
         Third division on frontal region of cranium.

    4. Lateral pharyngeal dilator muscle: This single, paired muscle varied only in size from species to species. It was present in all species, and its points of origin and insertion were virtually identical in all.

    5. Medial pharyngeal dilator muscle: Variations:

A: Muscle present.
    A.1: Paired.
    A.2: Unpaired.
B: Muscle absent.

Table I

PUMP MUSCLE CHARACTERISTICS

	Muscle 2	Muscle 3	Muscle 5
Sphinginae:			
Manduca sexta	C	A.3	A.1
Ceratomia undulosa	C	A.1	B
Ceratomia catalpae	C	A.2, B.1*	A.1
Sphinx eremitus	B	C.2	A.2
Smerinthinae:			
Smerinthus geminatus	A	C.2	A.1
Paonias excaecata	A	A.4	B
Paonias myops	A	B.3	B
Cressonia juglandis	A	C.1	B
Pachysphinx modesta	A	C.1	B
Macroglossinae:			
Haemorrhagia thysbe	B	B.4	B
Haemorrhagia diffinis	B	B.4	A.1
Philampelinae:			
Pholus satellitia	A	B.4	A.1
Ampeloeca myron	C	B.2	A.1
Amphion nessus	C	B.4	A.1
Choerocampinae:			
Celerio lineata	A	A.2	A.1

*Considerable variation

Table II

NUMBER OF ANTENNAL, LABIAL PALP, AND PROBOSCIS EXTENSOR

MUSCLES

	Antennal Muscles	Palp Muscles	Proboscis Ext. Muscles
Sphinginae:			
Manduca sexta	5	2	3
Ceratomia undulosa	4	2	3
Ceratomia catalpae	4	1	2
Sphinx eremitus	5	2	3
Smerinthinae:			
Smerinthus geminatus	4	1	1
Paonias excaecata	4	1	1
Paonias myops	4	1	1
Cressonia juglandis	5	1	1
Pachysphinx modesta	4	1	1
Macroglossinae:			
Haemorrhagia thysbe	5	2	3
Haemorrhagia diffinis	5	2	3
Philampelinae:			
Pholus satellitia	5	2	3
Ampeloeca myron	5	2	3
Amphion nessus	5	2	3
Choerocampinae:			
Celerio lineata	5	2	3

Table III

PROBOSCIS LENGTH

Number after specific name represents number of specimens examined. (*) indicates moths not selected for internal dissection. Lengths are in millimeters.

	Range	Average
Sphinginae:		
Manduca sexta (5)	66-93	80.0
Manduca quinquemaculata* (2)	87-93	90.0
Ceratomia amyntor* (2)	11-13	12.0
Ceratomia undulosa (5)	9-11	9.8
Ceratomia catalpae (5)	4-5	4.4
Sphinx eremitus (3)	38-40	39.0
Sphinx chersis* (2)	41-51	46.0
Sphinx kalmiae* (1)		40.0
Sphinx drupiferarum* (1)		44.0
Smerinthinae:		
Smerinthus geminatus (5)	2-3	2.9
Paonias excaecata (5)	3-4	3.4
Paonias myops (5)	2-3	2.6
Cressonia juglandis (4)	2-3	2.5
Pachysphinx modesta (5)	3-5	4.0
Macroglossinae:		
Haemorrhagia thysbe (5)	18-20	19.4
Haemorrhagia diffinis (2)	17-17	17.0
Philampelinae:		
Pholus satellitia (2)	33-36	34.5
Ampeloeca myron (3)	14-15	14.7
Deidamia inscriptum* (3)	13-14	13.3
Amphion nessus (5)	15-17	16.0
Choerocampinae:		
Celerio lineata (5)	34-41	37.0

DISCUSSION

It is clear from the morphological and field evidence presented that many species of sphinx moths have lost their ability to feed as adult insects. It is apparent that none of the Smerinthinae examined could possibly feed. Their morphological equipment is simply not adequate. Their lack of two pairs of proboscis extensor muscles, and the reduction of the proboscis are noteworthy. It is surprising to find only one or two statements in the literature that indicate the lack of ability of moths of this subfamily to use the proboscis. Rothschild and Jordan (1907) state:

"Rüssel nie uber den Hinterleib hinausragend, zuweilen
zu zwie ganz kurzen Lappen verkümmert, bei den meisten
Arten nicht mehr als ein Saugorgan brauchbar."

Others, including Forbes (1948) and Holland (1941) indicate the reduced proboscis in this group, but say nothing about its function.

It is clear, also, that certain members of a typically feeding subfamily, Sphinginae, are non-feeders. Members of the genus Ceratomia considered in this investigation are certainly not capable of taking food, but these insects are non-feeders for partly different morphological reasons, than is the case in the Smerinthinae. While Ceratomia shares the reduced mouth parts of the latter, there is only reduction in the size, not loss, of the proboscis extensor muscles in C. undulosa, all three typical pairs of muscles being present, and reduction in size as well as loss of one set of muscles in C. catalpae. The possibility of the three muscles still being useable cannot be ruled out, but in Ceratomia the sucking pump and its associated muscles have become so reduced that it is apparently incapable of functioning.

C. catalpae deserves some special attention for in that species, where the tendency to lose functional feeding apparatus is more advanced than in C. undulosa, there is, considerably more individual variation of muscles associated with the sucking pump than in any of the other sphingids studied. Possibly this species is presently in a state of losing these muscles, since some individuals have fewer and/or smaller muscles than others. It has apparently not yet reached a fixed genetic state as have other non-feeding species.

Little is known about sphingid ancestry and nothing was uncovered in the literature concerning it. It must be pointed out that any conclusions in this respect, in the present paper, are somewhat hypothetical. Any morphologist reaches his evolutionary conclusions with various degrees of validity. It may be stated, for instance, that such and such a structure was derived from a more primitive type that may have had certain features. The conclusions made in this respect are apt to reach a higher degree of validity in proportion to the amount of observation the worker has made on the modifications of the structure as it occurs in a long series of species that possess the structure.

The attempt has been made to show muscle homologies in sphinx moths and while it would be presumptuous to base a phylogeny of sphingid subfamilies just on the basis of head muscles and cranial structure, it is possible, I feel, to point out some relationships.

It is an accepted assumption among morphologists that muscles may split, drop out, and change origins. It can be assumed that the sphingid ancestor was a feeding creature, with a full complement of head muscles

associated with feeding. From that ancestry there branched one group which are all non-feeders; the Smerinthinae, whose head muscle complement is no longer complete. These moths are distinctly set apart from other sphinx moths on this basis and other aspects of the head.

From a feeding line, more recently in time probably, there branched from another subfamily of typical feeders, a small group of non-feeders; the genus Ceratomia of the Sphinginae (other genera, including Lapara which has a much reduced proboscis, might fit in this group also). In Ceratomia the tendency to lose feeding abilities is less advanced than in the Smerinthinae, and, in part, for different morphological reasons as has been already noted. The plastic evolutionary state, as evidenced by C. catalpae, in regard to loss of feeding ability and modification of head muscles concerned, is noteworthy. It demonstrates, at least, what steps might have been taken by other sphinx moths as they "advanced" from a feeding to a non-feeding state. Namely loss of muscles, reduction in size of muscles, reduction in the size of the sucking pump (not in Smerinthinae) and proboscis reduction.

The Macroglossinae, Philampelinae, and Choerocampinae would, on the basis of head muscle configuration seem rather closer to one another than to the other subfamilies, and closer to the Sphinginae than the Smerinthinae.

It seems probable that the most generalized condition within the sphinx moths would be a situation wherein the sucking pump was moderately to well developed, the proboscis was moderately developed, one undivided, and two paired sets of cibarial dilator muscles were present, two pairs of pharyngeal dilator muscles were present, three pairs of proboscis extensor muscles were present, two pairs of labial palp muscles and five pairs of antennal muscles were present. Divergent plans which may be considered progressive rather than conservative, include a reduction of the length of the proboscis as in Ceratomia and the Smerinthinae, or a more extensive development of that organ as in Manduca, a reduced sucking pump development as in Ceratomia, division of the cibarial dilator muscles, reduction in the size of the latter, dropping out of one or more sets of muscles, as in the proboscis extensor muscles of Smerinthinae, loss of one set of labial palp muscles, and loss of one set of antennal muscles.

If these criteria are born in mind, the moths of the subfamily Smerinthinae must be considered most divergent from the basic plan and, with reference to their head morphology at least, the least primitive.

SUMMARY

The morphology of the head musculature of 15 species of sphinx moths, representing five subfamilies was studied. Special emphasis was placed of the muscles associated with feeding mechanisms. Endo- and exoskeletal structure of the cranium was considered wherever necessary.

Four points are to be stressed by way of conclusion:

1. In the generalized sphinx moth head a maximum of 18 muscles may be found, exclusive of intrinsic proboscis and antennal muscles. Most of the muscles are paired. The muscles have been classified into the following six groups: 1) the dilator muscles of the sucking pump, 2) the muscles of the wall of the sucking pump, 3) muscle of the salivarium,

4) proboscis extensor muscles, 5) antennal muscles, and 6) muscles of the labial palps.

The dilator muscles of the sucking pump are always present, but may be divided or reduced in size or number. The most anterior of these muscles is never paired but the others always are except for the most posterior one which is sometimes unpaired or absent. The latter is the only muscle of this group ever to drop out. Muscles of this group dilate the sucking pump.

Muscles of the wall of the sucking pump are always present but may be reduced as in the moths of the genus Ceratomia. These muscles constrict the pump.

Muscles of the salivarium are always present but may be reduced, as in all Smerinthinae. These muscles exert forces on the salivarium which presumably control its secretions.

The proboscis extensor muscles may be reduced to one set, as in all Smerinthinae, or two sets, as in C. catalpae. All other sphinx moths examined had three sets, but these may be reduced as in C. undulosa. These muscles exert forces on the stipes which may press blood into the outer lumen of the proboscis, thereby extending it.

The antennal muscles are well developed in all species and consist of four or five sets. Two sets elevate the antennae and three sets depress them. Four sets were found in most Smerinthinae and in the genus Ceratomia.

The muscles of the labial palps occurred in two sets in most species, but only one in C. catalpae and the Smerinthinae. These muscles depress, elevate, and move the palps outward.

2. Loss of the necessary feeding musculature, reduction of the proboscis, and correlated field observations indicate that members of the subfamily Smerinthinae, and of the genus Ceratomia (Sphinginae) do not feed as adults.

3. The sphinx moth ancestor was a feeding species. The furthest removed from the primitive type are members of the Smerinthinae. On the basis of internal and external cranial morphology the Macroglossinae, Philampelinae, and Choerocampinae show closer affinities with one another than with the Sphinginae, but the Sphinginae are more similar to them than to the Smerinthinae. If head morphology is considered, it may be assumed that Macroglossinae, Philampelinae, and Choerocampinae are closer to the primitive sphinx moth type than are the Sphinginae and Smerinthinae.

ACKNOWLEDGEMENTS

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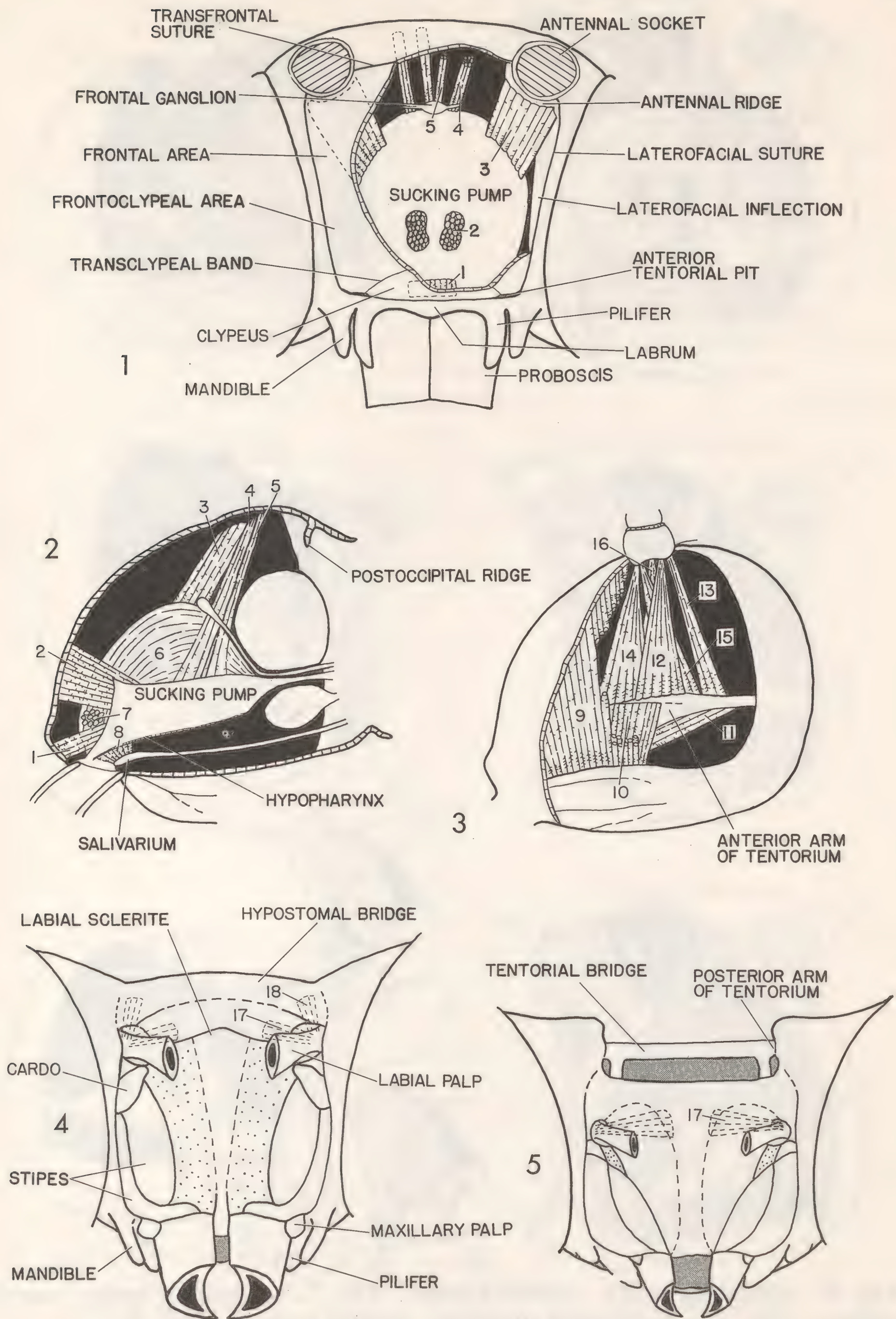
Fig. 1.--Generalized cranium, frontal aspect with portion of frontal sclerite removed. Fig. 2.--Generalized cranium, sagittal aspect.
Fig. 3.--Generalized cranium, lateral aspect with left eye removed.
Fig. 4.--Generalized cranium, ventral aspect. Fig. 5.--Paonias myops, ventral aspect.
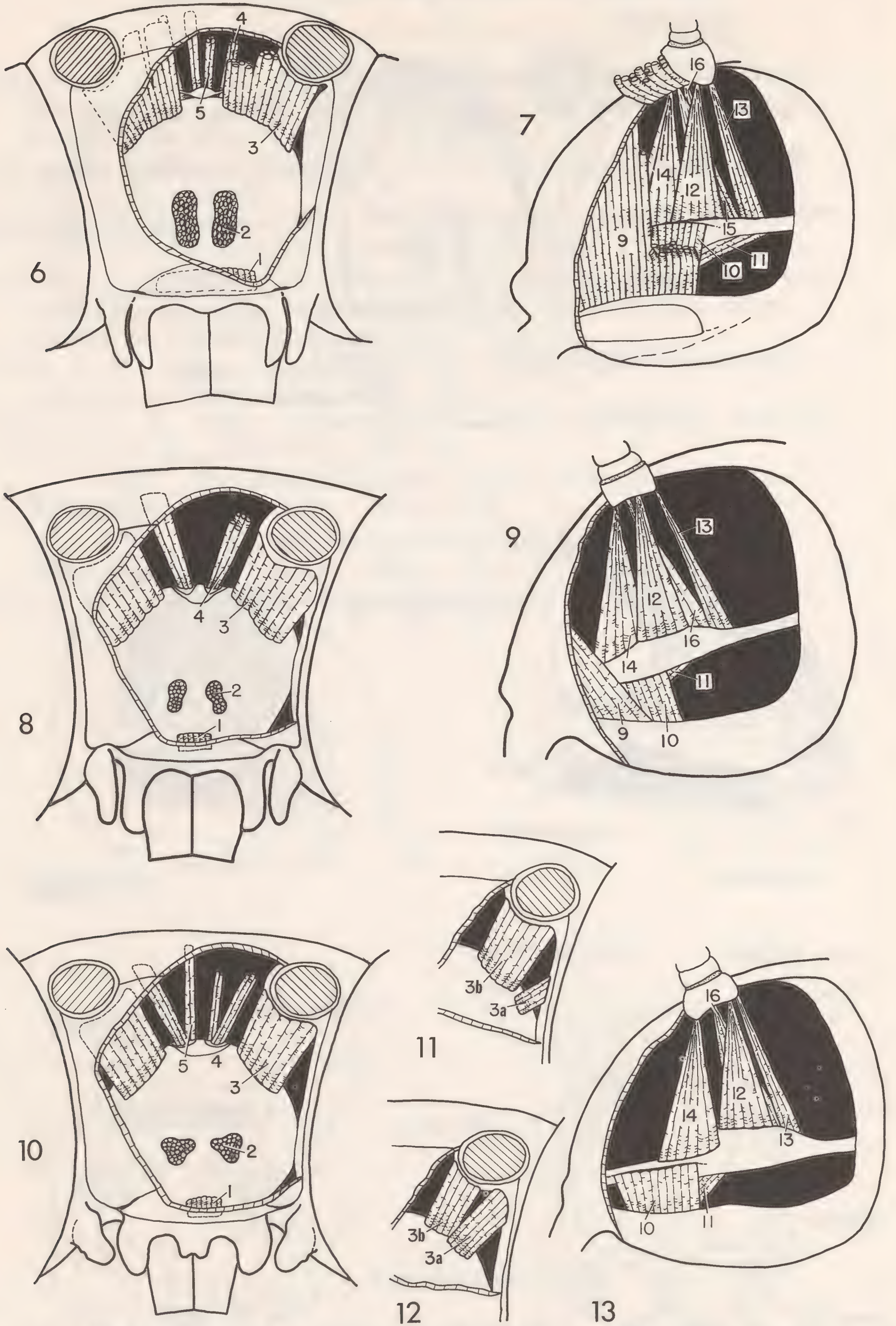
Fig. 6.--Manduca sexta, frontal aspect. Fig. 7.--Manduca sexta, lateral aspect. Fig. 8.--Ceratomia undulosa, frontal aspect. Fig. 9--Ceratomia undulosa, lateral aspect. Fig. 10.--Ceratomia catalpae, frontal aspect. Fig. 11.--Ceratomia catalpae, frontal aspect showing variations in muscle 3. Fig. 12.--Ceratomia catalpae, frontal aspect showing variations in muscle 3. Fig. 13.--Ceratomia catalpae, lateral aspect.
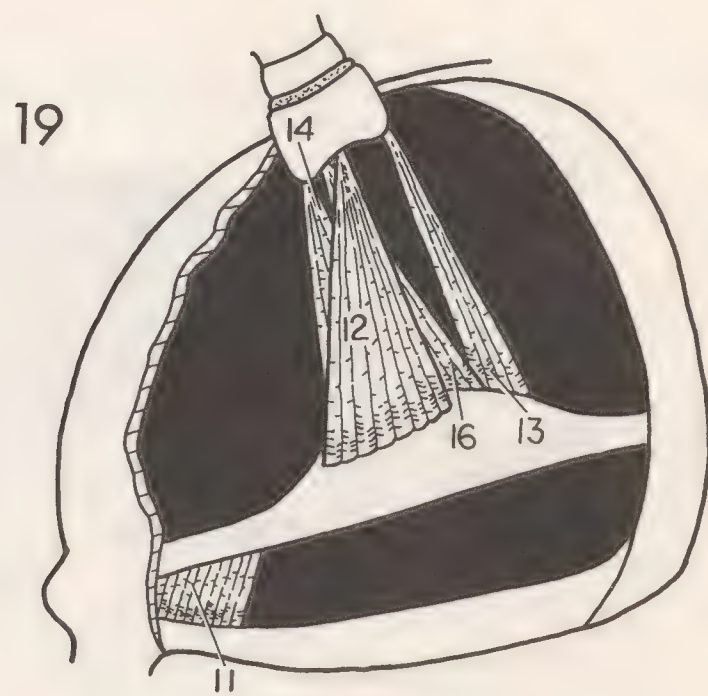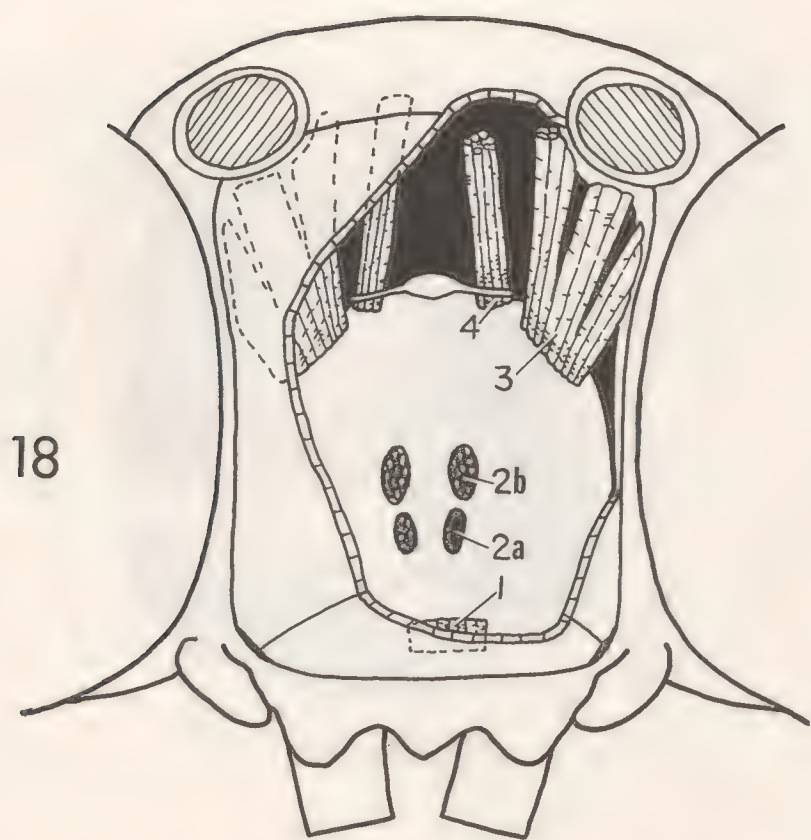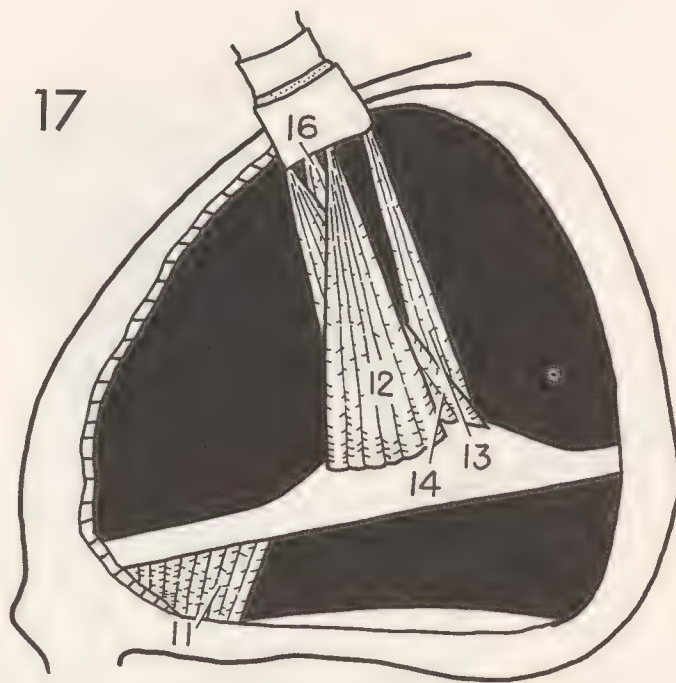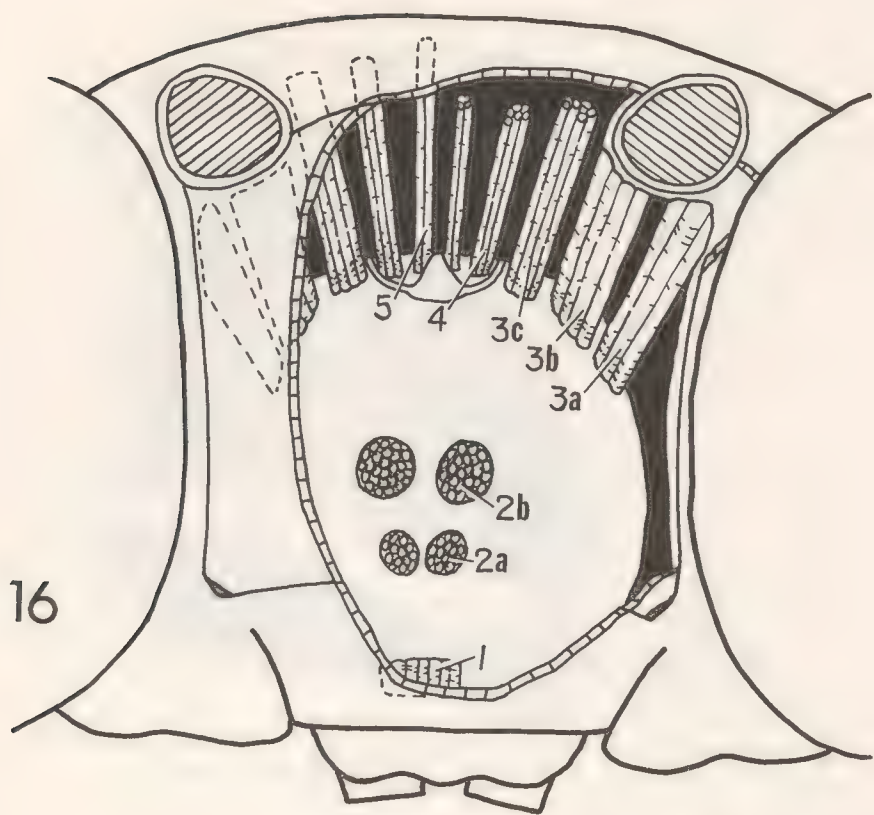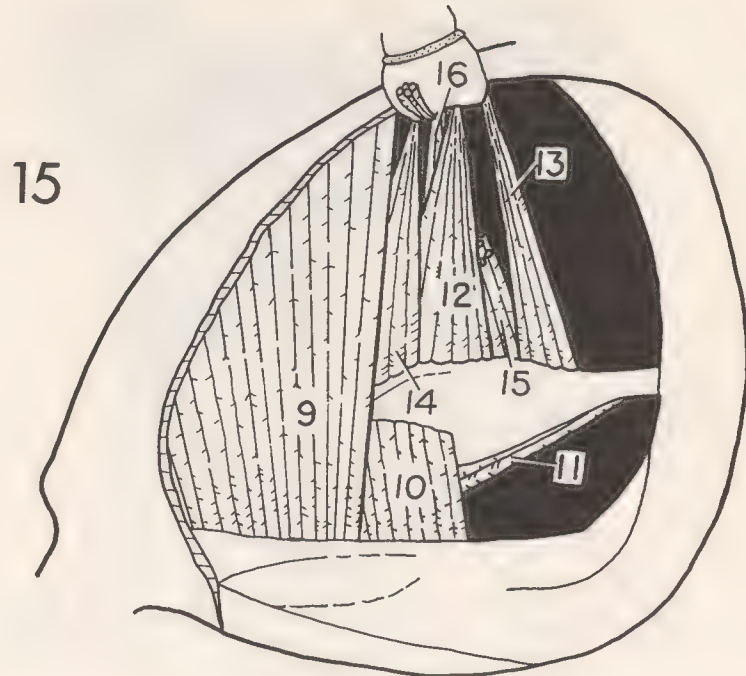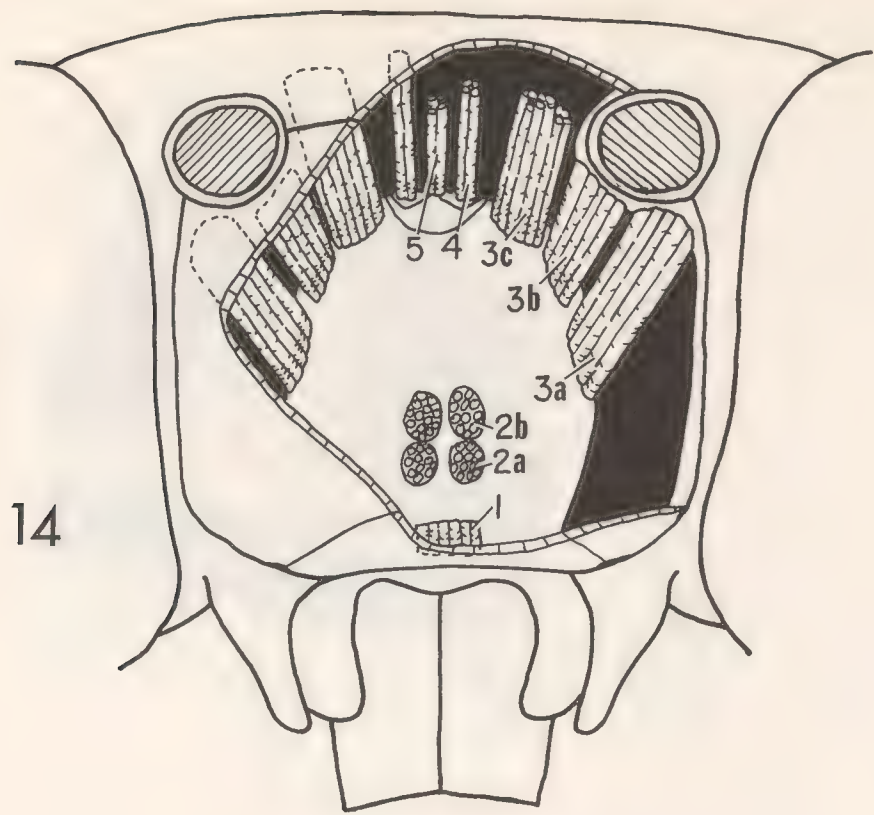
Fig. 14.--Sphinx eremitus, frontal aspect.   Fig. 15.--Sphinx eremitus, lateral aspect.   Fig. 16.--Smerinthus geminatus, frontal aspect. Fig. 17.--Smerinthus geminatus, lateral aspect.   Fig. 18.--Paonias excaecata, frontal aspect.   Fig. 19.--Paonias excaecata, lateral aspect.
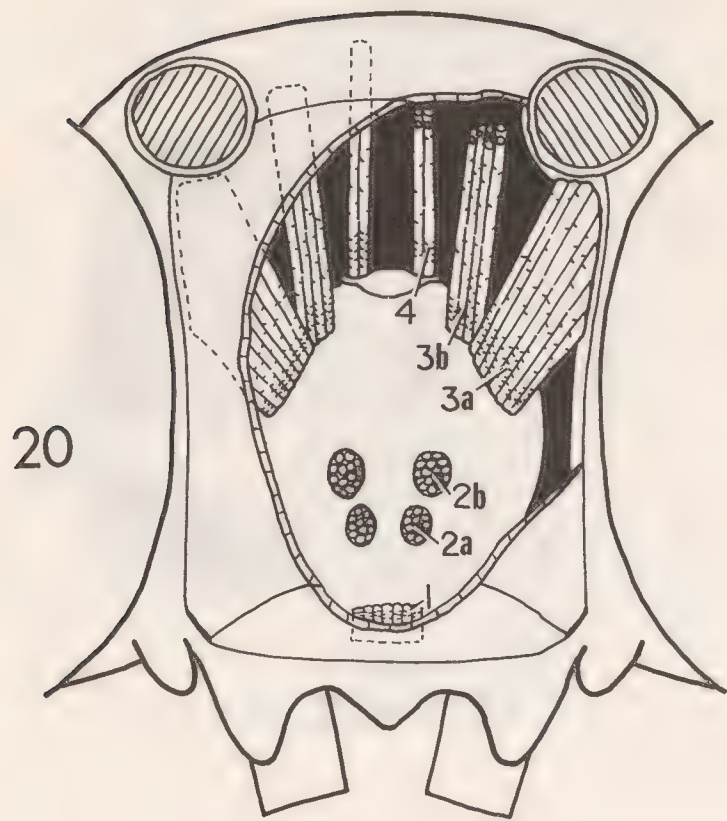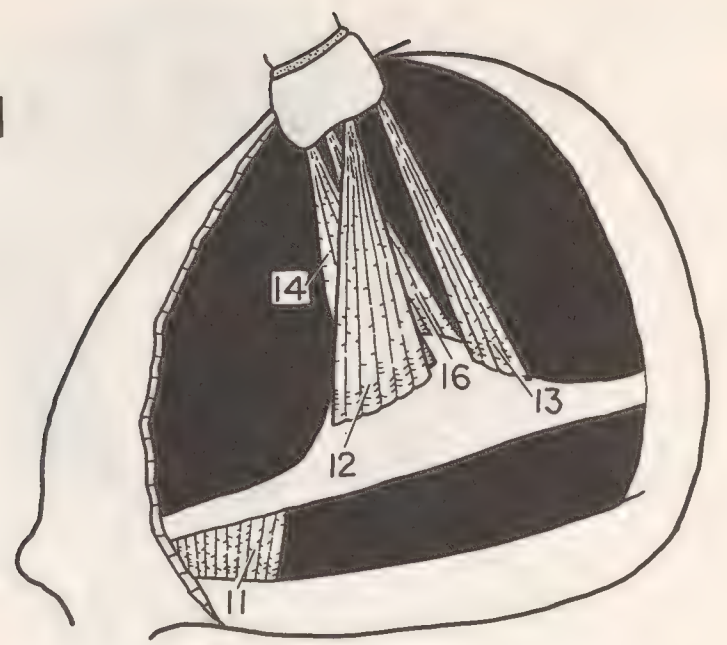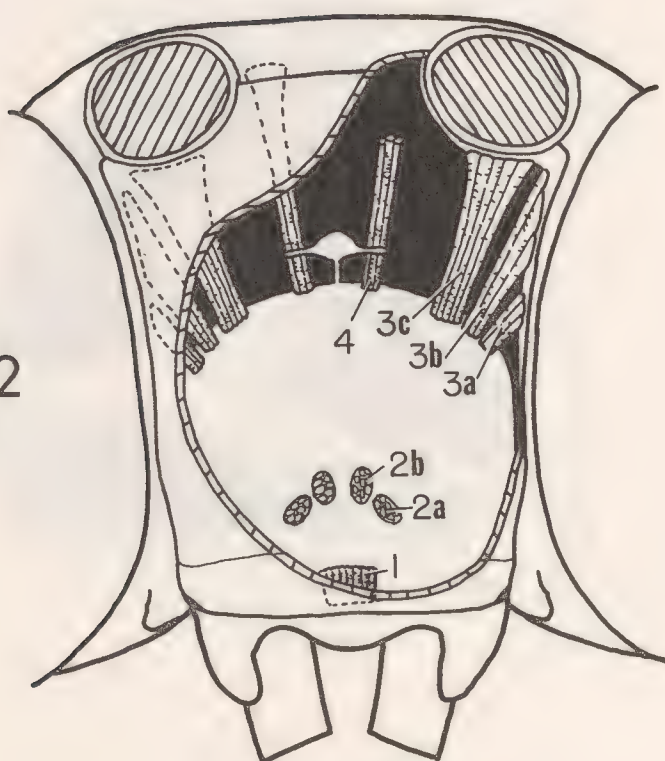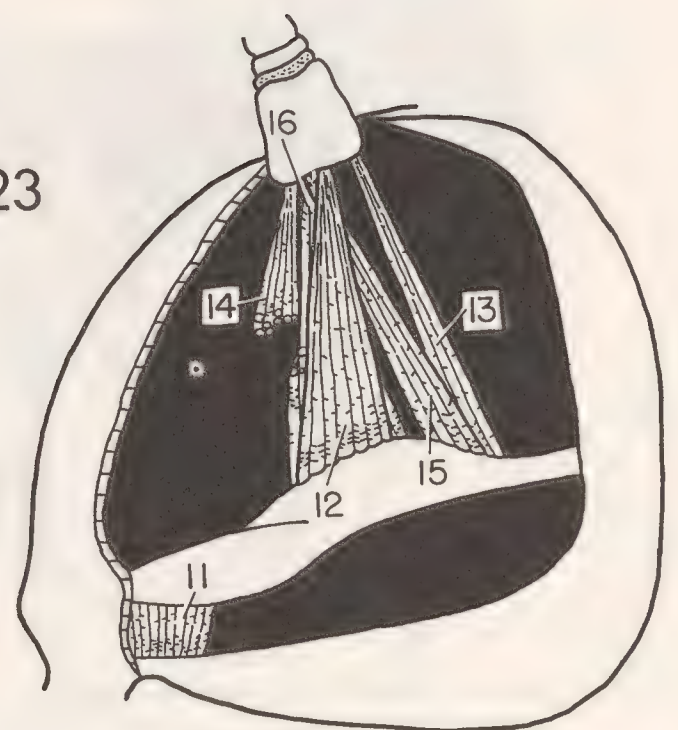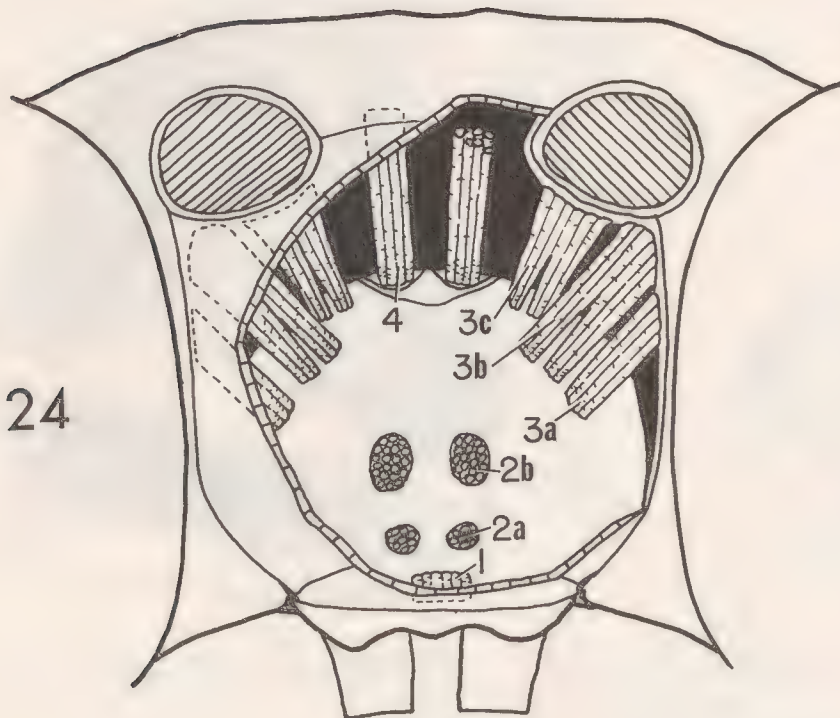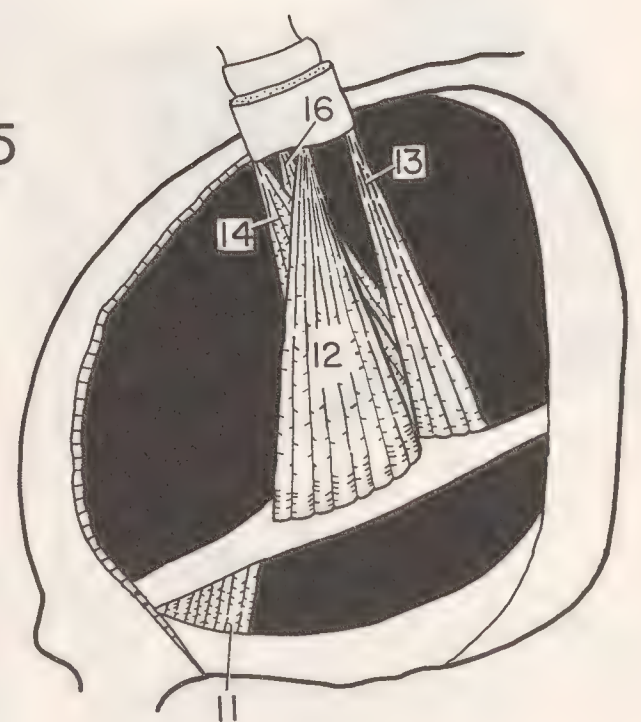
Fig. 20.--Paonias myops, frontal aspect. Fig. 21.--Paonias myops, lateral aspect. Fig. 22.--Cressonia juglandis, frontal aspect. Fig. 23.--Cressonia juglandis, lateral aspect. Fig. 24.--Pachsphinx modesta, frontal aspect. Fig. 25.--Pachsphinx modesta, lateral aspect.
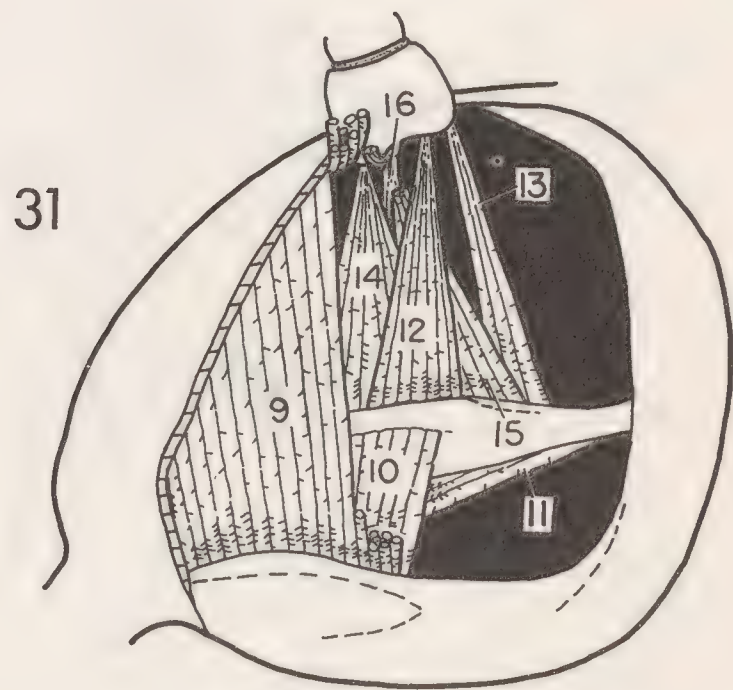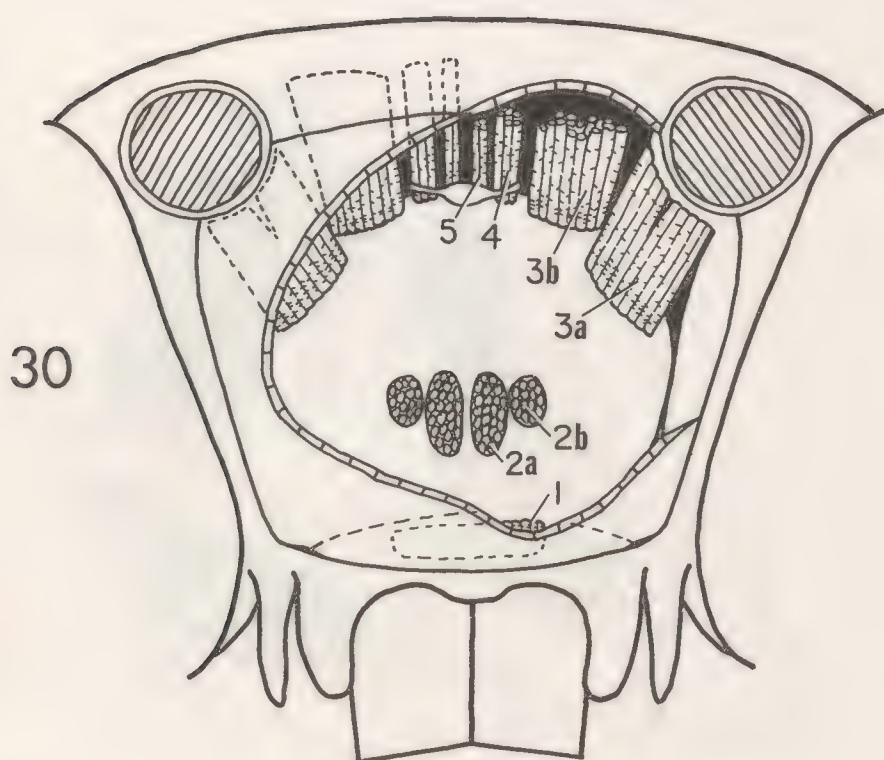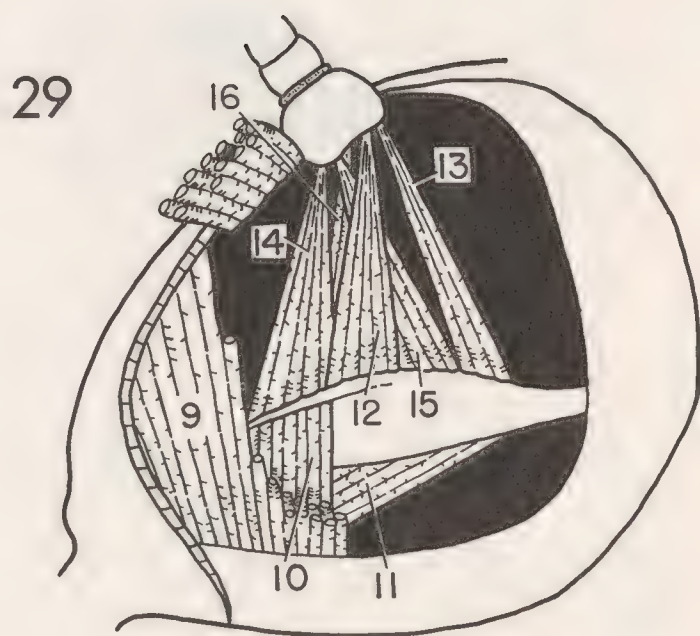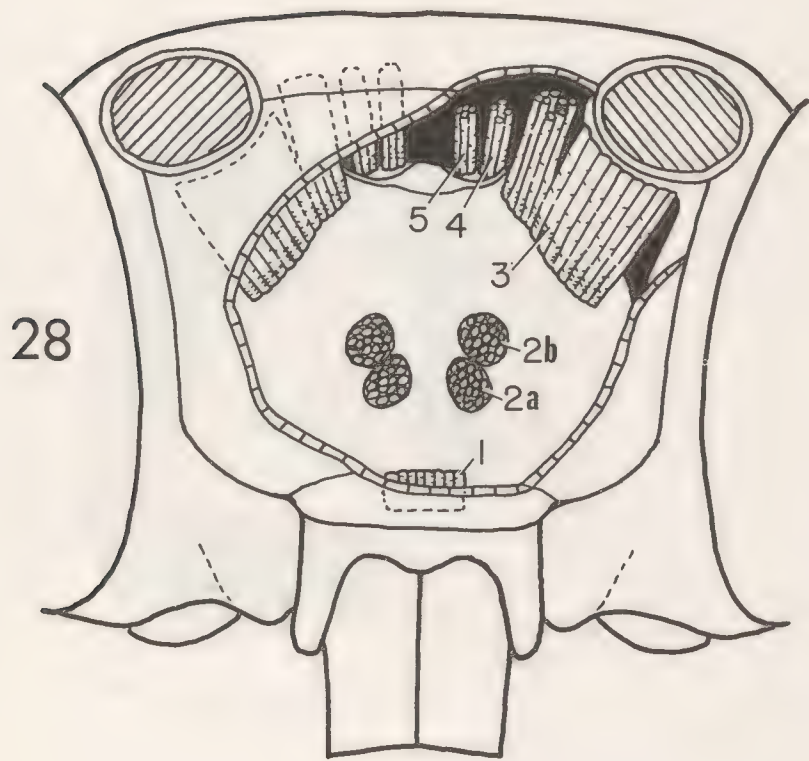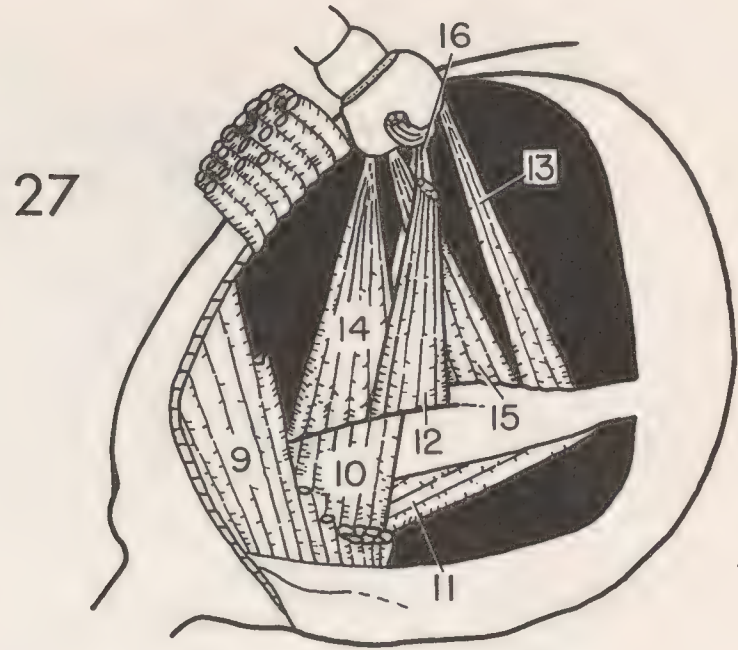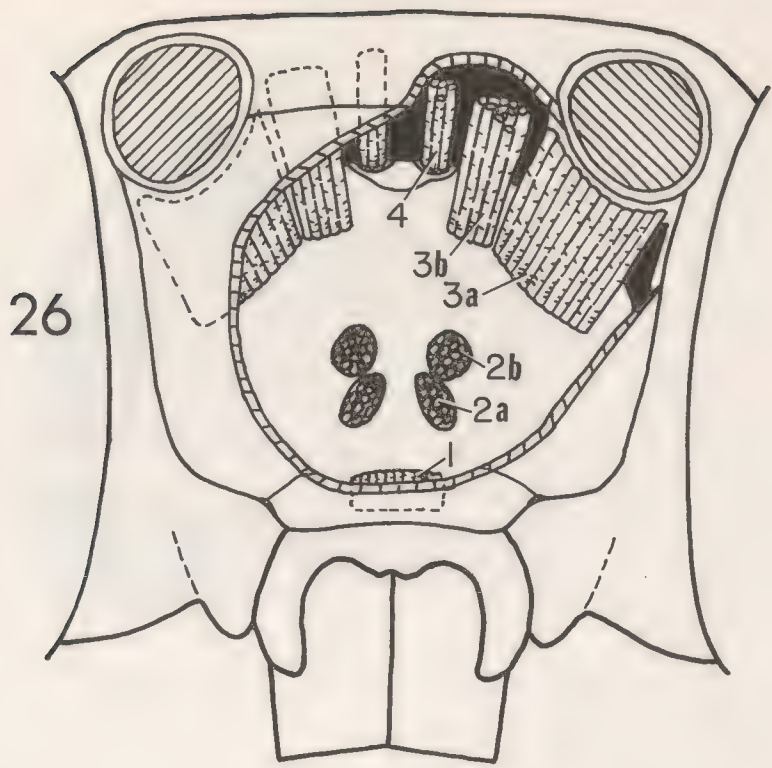
Fig. 26.--Haemorrhagia thysbe, frontal aspect. Fig. 27.--Haemorrhagia thysbe, lateral aspect. Fig. 28.--Haemorrhagia diffinis, frontal aspect. Fig. 29.--Haemorrhagia diffinis, lateral aspect. Fig. 30.--Pholus satellitia pandorus, frontal aspect. Fig. 31.--Pholus satellitia pandorus, lateral aspect.
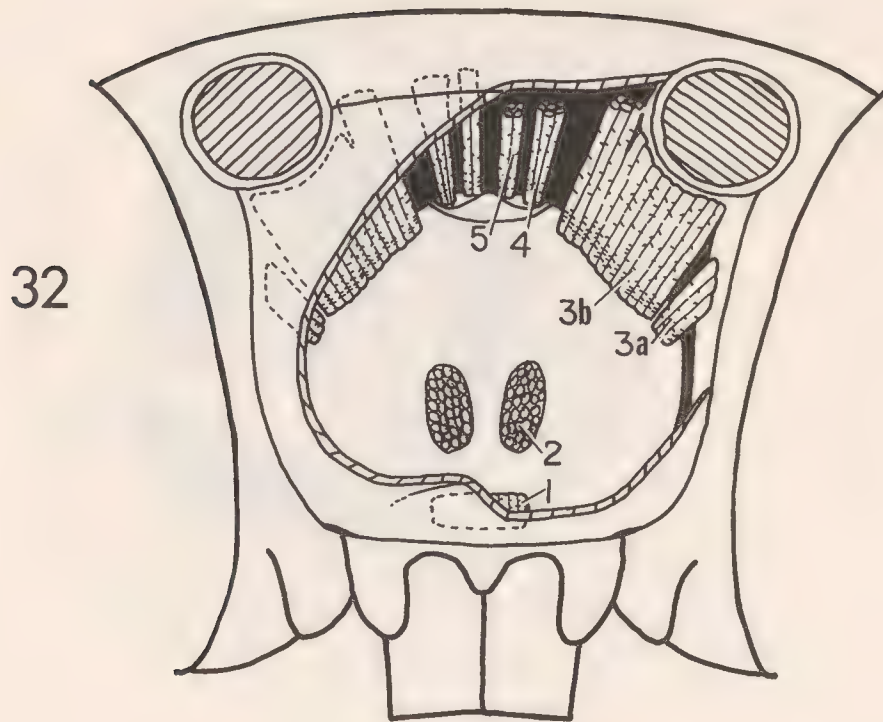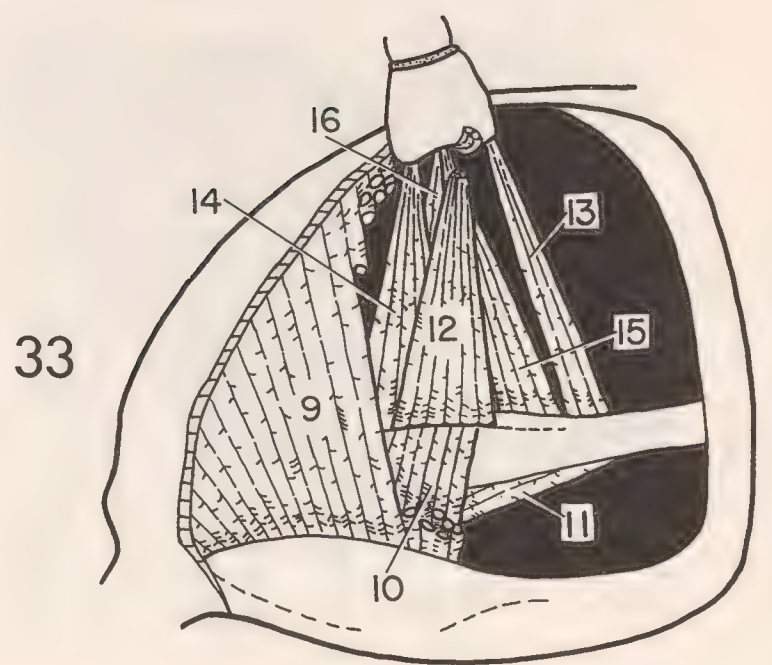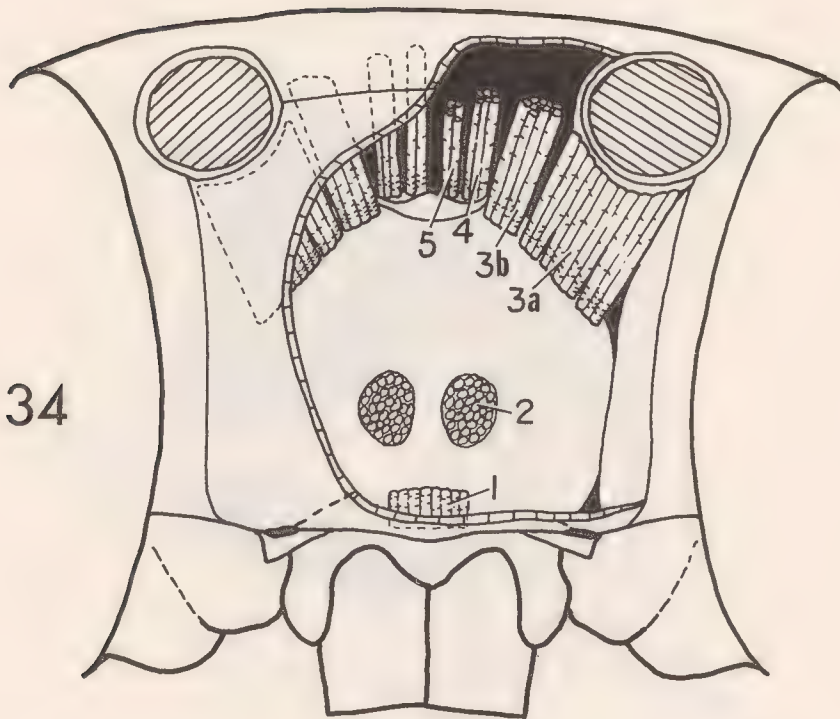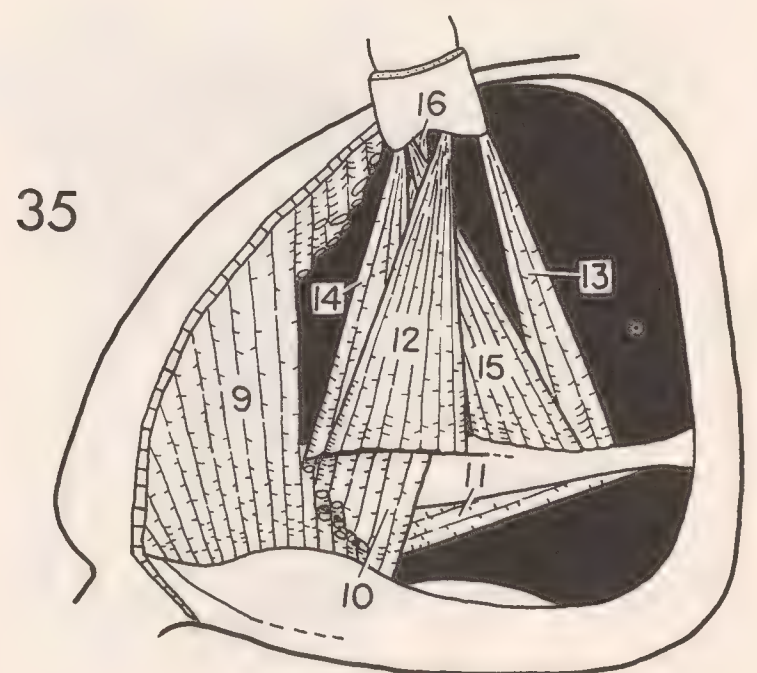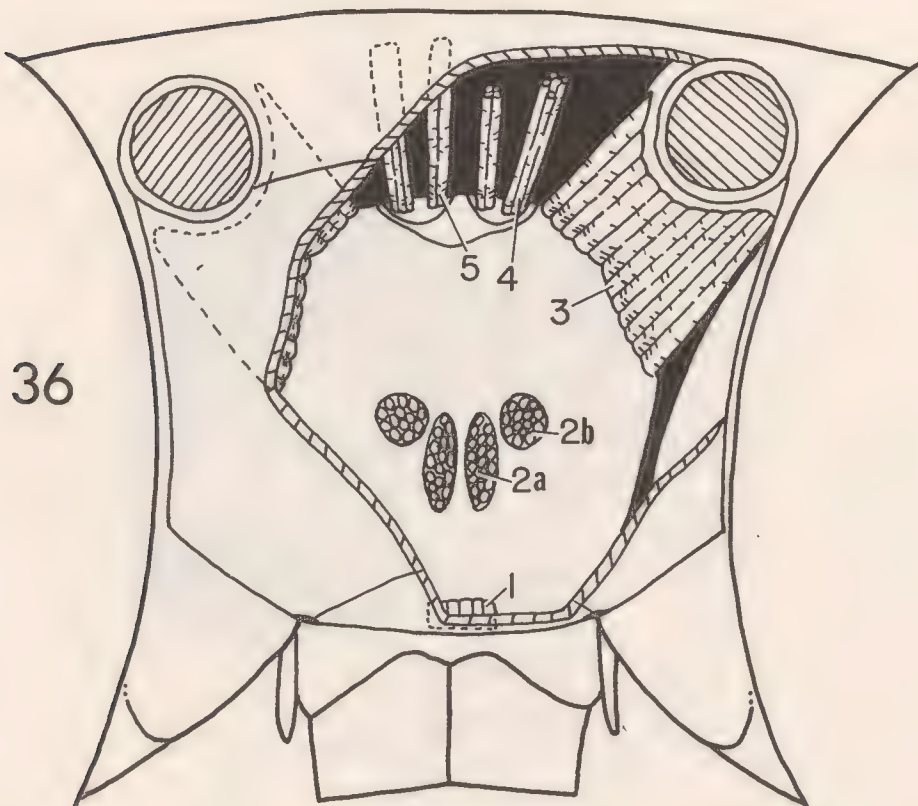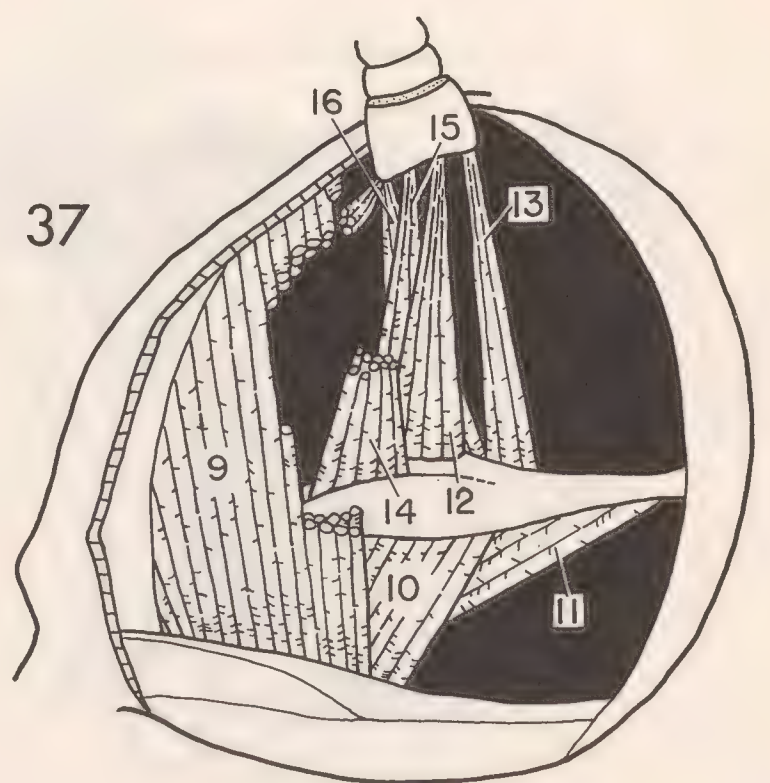
Fig. 32.--Ampeloeca myron, frontal aspect.   Fig. 33.--Ampeloeca myron, lateral aspect.   Fig. 34.--Amphion nessus, frontal aspect.   Fig. 35.-- Amphion nessus, lateral aspect.   Fig. 36.--Celerio lineata, frontal aspect. Fig. 37.--Celerio lineata, lateral aspect.